

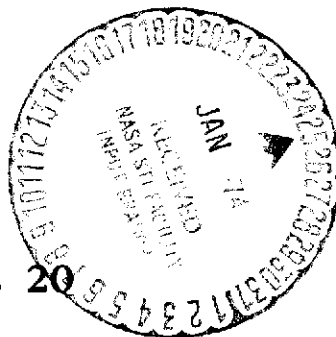
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Mathematical Models of Biological Systems

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| 16. Abstract Well-known mathematical models are used to model population associations, biocoenoses, biogeocoenoses and artificial biological associations. The optimal yield concept is defined in relation to the optimal productivity of an association. The optimal productivity problem is solved for the simplest types of associations, such as a homogeneous population in a chemostat and also in more complex cases, for example, for an association of the "predator-prey" type. The simplest models are generalized to cases in which it is necessary to take into consideration the distribution of individuals in the population by age, size, etc. The models are described by systems of differential equations. The optimal policies are obtained using dynamic programming methods, nonlinear programming methods and the Pontryagin maximum principle. Optimal steady state strategies are also obtained. | | | |
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The book presents existing mathematical models of biological population associations, biocoenoses and biogeocoenoses and biological associations. The authors solve the optimal productivity problem for the simplest associations, such as a homogeneous population, a population cultivated in a chemostat, and also present solutions for a more complex problem--the optimization of the productivity of an association of the "predator-prey" type. Stationary yield collection processes, problems of regulating the trophic structure are discussed, and the models presented are generalized to the case when it is necessary to take into account the age distribution of individuals, the distribution by size, etc. One chapter is devoted to continuous yield collection models, and the general maximum yield theorem is proved. The results obtained are analyzed on the example of the problem of creating stable artificial biological associations. Some new measures of stability are proposed. Possible criteria for the reliability of biological life support systems are discussed

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MATHEMATICAL MODELS OF BIOLOGICAL SYSTEMS

Yu. M. Svirezhev, Ye. Ya. Yelizarov

INTRODUCTION

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An association of live organisms together with their habitat which is restricted by certain natural boundaries and which has one or several stable states is usually called a biogeocoenosis (BGC). The BGC concept was introduced for the first time in the work of V. N. Sukhachev. Today biogeocoenology refers to those new advanced directions in contemporary natural science that developed through the contact of many sciences, which are of great theoretical importance and are the scientific basis for the development of many branches of the national economy and the rational use of natural resources.

A deep and multifaceted study of the various interrelationships and interdependences which determine the life and the productivity of the BGC which make it possible to control and perfect them, is not possible without using exact quantitative methods. Recently mathematical planning and control methods have been used widely in industry and economics, in areas which are intimately related to human work activity. The concepts "optimal schedule," "optimal policy" and other concepts have come into wide use. When industrial processes and economic interrelations are planned, an attempt is made to take into account the interrelation among many factors, and to select not only a good schedule for the operations but the best schedule which is "optimal" with respect to some criterion. Unfortunately, only in the last few years man became aware of the necessity to model his interrelations with nature in an optimal manner, since natural resources are not "inexhaustible."

We will give an interesting example. It is known that the number of industries in any population of live organisms whose size is bounded above by a certain limiting factor (the amount of food, the region where it dwells, etc.) varies in accordance with the logistic law (Fig. 1). The limiting factor has no particular effect on the initial segment (ab) of the curve, and no matter how bad the effect of the population on its environment (excluding, of course, very extreme cases), this effect is so small that it has practically no influence on the population limit and on the environment. The picture changes considerably when the population lies on the segment of the curve where the rate of growth attains its maximum value (the segment bc). Here the effect of the limiting factor is already felt, the population has already a considerable effect on the environment, and, hence, the reverse effect is also considerable. The result of a "bad" effect of the population on the environment is, as a rule, a reduced population size limit.

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And now, along with Fig. 1 we will show the graph according to which the earth's population size changes over time. It can be seen from Fig. 2 that we have already entered the second growth stage, and that the problem of reducing the "harmful" effect of man on his environment is a pressing problem which cannot be postponed. The majority of natural BGC are, at the present time, systems which have already been formed, which are in a state of dynamic equilibrium. Man, as a result of his economic activity interferes with natural BGC and disturbs the existing equilibrium, often by far not in the most favorable direction, or he tries to create certain artificial biogeocoenotic systems. Therefore, the question arises naturally of how to act on the BGC in a controlled manner, so that the action is optimal with respect to some criterion.

One of the possible criteria which can be used is the maximization of the yield, i.e., the maximum biological productivity of coenoses with additional constraints which make it possible to preserve the BGC itself. From this point of view, our book is devoted to the application of the mathematical methods of optimization theory which have already been developed sufficiently well, to objects and models which for all practical purposes were not studied using these methods, namely to biogeocoenoses and their quantitative models.

In 1968 the book "Ecology and Resource Management: A Quantitative Approach," by Kenneth E. F. Watt was published in the USA.¹ A large part of this book discusses the consequences of man's interference in natural associations. After this the author discusses various quantitative models of these processes (mainly models of the Volterra type and empirical models). As a matter of fact, the system, or even science developed by him, can be called ecology engineering; and in our terminology, engineering or applied biogeocoenology. Given the generality of our objectives, the approaches of Watt and those of the authors of this book differ to a considerable extent. Watt collected practically all special methods and models which were used until now in the quantitative modeling of natural associations and the processes of their use. Trying to introduce a certain unity into the discussion, he uses widely a technique, which is usually called today "the systems approach." The interesting chapter on the application of an electronic digital computer to processing ecological observation data stands somewhat apart. /7

Our book is several times smaller in scope, and naturally also smaller in the number of topics discussed and less varied in the methods used. However, it seems to us that we gained in the unity of the presentation, of course, at the expense of generality clarity, and perhaps even interest.

1. Watt, Kenneth E. F., "Ecology and Resource Management: A Quantitative Approach," N. Y., McGraw-Hill Book Co., 1968, 450 pp

The problem of modeling biological systems and their optimal use has still another aspect which is connected with the creation of an "earth" environment for man in space and on other planets. The creation of permanent scientific stations in space and on planets in the solar system is a natural stage in the evolution of space travel, and contemporary trends give us reason to believe that the implementation of this stage can begin in the nearest decades. We point out, that according to the forecasts of a number of NASA workers which were made at the symposium of the American Astronautical Society in 1966, a permanent scientific base will be erected on the moon in 1982-1985, and the erection of permanent scientific bases on Mars and even on Mercury and the Galilean satellites of Jupiter are to be expected in 1990-2000. These forecasts which were made in the period when work on the USA space program was most intense and when it was most generously financed, are apparently overly optimistic. However, there can be no doubt that the characteristics of space rocket systems which will be constructed within the next 10-20 years, in their weight and power aspects, will make it possible to carry out the projects which were mentioned above.

One of the most important conditions for the successful development and functioning of permanent stations is the development of highly efficient and reliable life support systems. For stations which are remote from earth and which are situated on natural celestial bodies, an important requirement is the high degree of their autonomy, and consequently, a long operational time (T) of the system. Provisionally an estimate for this time is $T \geq 10^3$ days. For such operational times when the crew is 10 people or more, closed ecological systems have the greatest promise. It can also be assumed that systems of the type mentioned above, can also be used advantageously in large orbital observatories in near space, since a certain relaxation of the requirements on the autonomy of the system will be compensated by greater requirements on its power, due to the increased size of the crew. /8

Thus, the development of principles for creating sufficiently powerful closed ecological systems, which we are fully justified in calling artificial microcosms, is a rather important and topical problem.

This problem can be solved in two ways: by simulating the stable biogeocoenoses which exist in the earth's biosphere, and by constructing entirely new types of biosystems using the basic laws which govern the functioning of the biogeocoenoses and the entire biosphere as a whole. However, in either of these two cases an important role in the development will be played by mathematical modeling, since the search for the optimum variants of the structures of coenoses and methods by which they can be efficiently controlled using full-scale experiments, is unrealistic both from the standpoint of the costs and also from the standpoint of the

deadlines which must be met.

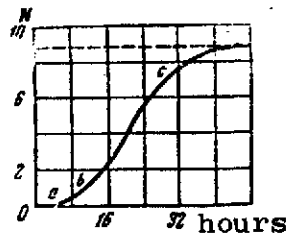


Fig. 1

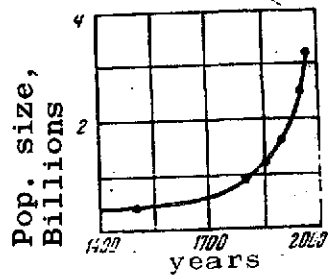


Fig. 2

Fig. 1. Population growth (N) of yeast cells (Gauze, 1934)

Fig. 2. World population growth ("Figures for socialist and capitalist countries," Moscow, IPL, 1966)

Chap. I. QUANTITATIVE MODELS IN BIOGEOCOENOLOGY AND PROBLEMS OF OPTIMAL YIELD

1. The Biogeocoenosis Concept. Biogeocoenosis and Ecological System--Two Different Concepts

The biogeocoenosis concept was introduced for the first time in the work of V. N. Sukachev (Sukachev, 1945, 1947, 1949, 1964, 1966). In historical perspective, biogeocoenosis (BGC) is an association of organisms which adapt to one another and to their surrounding environment in the evolutionary process and communicate with one another and with the environment through various channels through which mass, energy, and information flows circulate. The relations among the organisms are either a direct or indirect consequence of the struggle for survival and natural selection in the given environmental conditions. Until the appearance of the work of V. N. Sukachev, the biocoenosis concept--an association of live organisms--was widely used. However, it makes no sense to study some biocoenosis apart from the environment in which it exists. Further, since any definition must be operational, rules must be given by which the biological association under consideration can be singled out. The first correct definition, biogeocoenosis, which sensibly singles out a biosystem was given by V. N. Sukachev, who pointed out the role of plant communities and landscape characteristics in the formation of stable biological associations. We note that many earlier biocoenological studies were in essence biogeocoenological. However, it was possible to operate with comparatively precise definitions only after the work of V. N. Sukachev. /9

One of the main difficulties which arises in the formulation of this type of borderline problems is the problem of terminology. Recently in biological studies more and more attention was given to a clear and contradiction-free formulation of basic concepts. Therefore, we will use for the basic set of terms the concepts which are widely used in biogeocoenology and ecology. However, sometimes a situation will arise in which the basic term is either too diffuse or too broad. In such a case we will not discard the term, we will only use it more formally and define it more precisely by introducing various types of constraints.

When we made our first attempts to study such problems, the idea occurred to us to divide almost the entire available literature on this problem into two large classes: the first class could be characterized by using the word "biogeocoenosis" as the fundamental concept, and the second by the phrase "ecological system." It seemed that here we had a purely terminological issue, since both these words denote the same concept. /10

Even more confusion was introduced by the fact that various authors who use these words always shift even if only slightly the meaning of the concepts which were defined. The fact which immediately draws our attention when we study various biological associations is that all members of the association are related to one another by various types of relations, i.e., every association has its own structure. The relations themselves in turn are channels of a kind over which mass, energy and information flows circulate. It is natural that when the initial concept was sought which would define such associations, the definition "ecological system" was adopted. Thus, "an ecological system" is a concept which is related to the structure of the association, in particular, the trophic structure. Spatial limitations are not essential for its definition.

When associations of organisms are studied it is necessary to take into account their environment, which has an important effect on the structure of the association. Between the organisms and the abiotic factors in the environment in which they live, various temperature, humidity, chemism, etc., connections are formed.

And finally the functional system which includes the association of live organisms and their environment is called an ecological system (ecosystem), (Odum, 1963; Macfadyen, 1965, DuVigneaud, Tang, 1968). The term "ecosystem" can be applied to biocoenoses and their environments which differ considerably in size:

- microecosystem (tree stump)
- mesoecosystem (meadow or grove)
- macroecosystem (ocean)

The unification of all ecological systems in the world leads to the concept of the giant earth ecological system, i.e., the concept of the biosphere.

When we single out an ecological system, the natural boundaries are not important to us. The ecological systems which can be studied are not only real existing stable associations, but any, even unstable, associations which need not have any unified structure. In the final analysis we always speak about the study of the formation, circulation, accumulation and transformation of matter, energy and information in processes connected with the activity of live organisms and their metabolism. No restrictions are imposed on the principles used to select ecological systems. Further, the size of the ecological system is unbounded above and below. The definition itself does not indicate in any way that the ecological system which is chosen must describe, to some extent, a real existing bounded natural system. Even though this is implicit.

in the requirement that the cycle be closed, nevertheless the basic concept is difficult to apply to problems of our type because of its excessive generality.

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We will now pass on to the biogeocoenosis concept. It arose out of the need to find somehow and isolate an elementary unit in the biosphere, which could be subdivided into these units without a remainder. In the definition given by N. V. Timofeyev-Resovskiy and A. N. Tyuryukanov (Timofeyev-Resovskiy, 1961; Timofeyev-Resovskiy, Tyuryukanov, 1966, 1967), it is said directly that a BGC is a sector of the biosphere through which no ~~essential~~ biogeocoenotic, geomorphological, hydrological, microclimatic and soil-geochemical boundary passes. Thus, the entire giant system, the earth's biosphere, is broken up into subsystems which are naturally separated from one another. As in the case of an ecological system, also here a certain system is singled out, about which it can be said that the principles used in singling it out are determined by natural limitations. This allows us to hope that the system studied has been singled out in the best possible way, and that the number and intensity of the relations within the region which was singled out are considerably larger than those between this region and the surrounding space. And the inevitable averaging of certain parameters of the system which takes place during subsequent study and simplification, is carried out over a set which is almost independent of the remaining sets, i.e., we have a system which is almost isolated. Of course, we can only speak about relative isolation, since the BGC themselves are unified in higher order systems (for example, geochemical landscapes) up to and including the biosphere.

One of the main characteristics of a BGC is the existence of dynamic equilibrium states of this system, and it is often said that we can only speak about a BGC when the system is in such a state (Timofeyev-Resovskiy, 1964). On the other hand the concept of an ecological system does not include the requirement of dynamic stability and the presence of equilibrium states. This point of view received unexpected support from W. R. Ashby (Ashby, 1966), when he talks about self-organizing principles. We quote his most characteristic statement: "Every isolated deterministic dynamic system which obeys fixed laws creates 'organisms' which are adapted to their 'surrounding environment.' The adaptation consists of a tendency toward equilibrium; it can be said, that in the process, the system makes a selection." Equilibrium in a simple system is usually trivial, but it can be very interesting and instructive in a complex multicomponent system such as a BGC. Notwithstanding the fact that equilibrium includes only a small part of all states, in a large system, this part is sufficiently large to ensure the necessary diversity. Suppose that the transition to such equilibrium is rather long. We find out that the existing states have the capacity to "survive" the changes caused by the laws. We will break the system in equilibrium into two parts, and we will call one part the "organism," or the

"association of organisms," or the "biocoenosis," and the other part the "surrounding," or "abiotic environment." We then find out that the "biocoenosis" is distinguished by its capacity to survive despite the disturbances in the "surrounding environment," i.e., the entire BGC is stable as a whole. The degree with which the entire system adapts to the environment, and the degree of stability are only limited by the dimensions of the entire dynamic system and by the time available to it to attain equilibrium.

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Thus, BGC are dynamic systems which were isolated naturally with relatively constant and deterministic laws, whose characteristic time is sufficiently large. The systems must have one or several stable states in which they "adapt" maximally to the surrounding environment. The environment itself must be part of the system as a whole.

And finally an applied aspect of this problem is of great interest to us. Since the BGC concept is based on real existing natural associations which are separated in space, the results obtained from the solution of applied problems based on this concept can be interpreted easily and uniquely. The matter is somewhat more complicated with ecological systems, since results obtained for an ecological system are more difficult to "connect" with some concrete natural association.

We note that recently these concepts have come closer to one another: often by an ecological system is meant precisely a BGC, and often a BGC itself is called an ecological system. This curious process shows how the general concept of an ecological system when it is concretely related to real existing objects no longer signifies at all, after a certain time, what it denoted when it was introduced.

2. Quantitative Models of Biological Associations

The first attempts to describe quantitatively biological associations were made in the work of Lotka (Lotka, 1920, 1923, 1925, 1932, 1934), Volterra (Volterra, 1926, 1928, 1931, 1935), and Kostitzin (Kostitzin, 1937). These models were constructed using the apparatus of differential equations. They took into account propagation and mortality factors and trophic interactions of one type or another.

For systems of the "predator-prey" type the trophic interactions were based on the method of "encounters," a certain analogue of collisions in kinetic gas theory, which assumes that the diet of the "predator" is proportional to the product of the number of the two types.

With the advent of electronic computers it was possible to model directly complex structures which closely approximate real BGC.

In the last years many articles appeared which were devoted to setting up quantitative models for sufficiently complex biocoenoses and to problems of controlled action on them (Lyapunov, 1966; Poletayev, 1966; Eman, 1966; Gil'derman, 1966; Gorstko, 1966, Gurfinkel', 1967, and others).

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A. A. Lyapunov emphasizes that a very useful theoretical way of studying certain biological problems is mathematical-machine modeling. Living nature as a whole is represented by it as a hierarchially organized system of objects with various organization levels. Every such object is split up into a number of objects on lower levels which are among themselves in a state of energy, material and information exchange. If the types of interactions among and within the individual classes of objects are known, it is useful to use the method of mathematical modeling to clarify the behavior of the system as a whole. In fact, taken as a whole the Earth's biosphere consists of many subsystems which are rather loosely connected (Vernadskiy, 1926; Sukachev, 1945, 1947, 1949; Timofeyev-Resovskiy, Tyuryukanov, 1966, 1967; Lyapunov, Stebayev, 1964) and these subsystems themselves consist of still smaller systems, which are again rich in internal relations but less rich in relations among themselves, etc. Speaking about the possibility of controlling the biosphere, A. A. Lyapunov notes, that the most suitable control object is a biogeocoenosis when it is considered as an elementary unit of the biosphere.

For practical applications (planning the rational utilization of natural arable land) the most important class of models is the class of portrait models (Poletayev, 1966) which are constructed with values of the parameters close to those which exist in nature. However, the construction of such models is beset by considerable difficulties because of a number of fundamental questions connected with the interaction mechanisms among the components of the biogeocoenosis, which is often a complex dynamic system. Therefore, it is more sensible to build simplified models of the search type for elementary situations within the confines of the biogeocoenoses, which in turn are used for building complex models of the portrait type.

Starting out with these assumptions, I. A. Poletayev constructed search models of biogeocoenoses. In doing this he follows Volterra and uses the apparatus of differential equations. By a component of the biogeocoenosis he means any substance which is simple or complex in composition, and any type of energy which is present and formed within the confines of the biogeocoenosis. Certain most essential BGC components are "critical" and are studied in an existing BGC as "narrow places." They determine the constraints which must be satisfied in order that the BGC function normally. Certain "types of activities" or "classes of activities" of the BGC components (basal metabolism, reproduction, acquisition of food, etc.) are also constraints. Thus the BGC dynamics (according to Poletayev) are described by a system of differential

equations for its "critical" components and a set of constraints on the "types of activities."

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Following the ideas of I. A. Poletayev, T. I. Eman (1966) studied the dynamics of certain models of biogeocoenoses. The central problem in these studies was the question of the presence or absence of BGC equilibrium states and stable conditions which differ little from these equilibrium states.

3. Types of Populations Models and the Optimum Catch Problem

One of the simplest associations of organisms is a population. Historically it so happened that fish populations have been studied sufficiently well quantitatively, especially populations of fish in fisheries, for which large amounts of statistical data were available.

In a survey article devoted to methods of modeling mathematically the dynamics of populations of fish in fisheries, V. S. Ivlev (1961) distinguishes two types of models: greatly simplified Thompson models (Thompson, 1937) and more sophisticated models, which use the apparatus of differential equations. Mathematical models which use the apparatus of differential equations in studies of fish populations were in turn classified by Gulland (Gulland, 1962) as follows:

- a) those which consider the population as a single whole, i.e., those which ignore the internal structure of the population. The Volterra (1931, 1935) and Gauze (1934) models can serve as examples;
- b) those which consider separately growth and stocking processes, in age groups and mortalities. Examples: the Baranov model (Baranov, 1918), the Russel model (Russel, 1931) and the fundamental model of Beverton and Holt, (1957);
- c) those which take into account the dependence of the growth and mortality coefficients on the population density (Tanaka, 1960);
- d) those which take into account the dependence of stocking in age groups on the population density. The Ricker model is an example (Ricker, 1958).

The dynamics of fish populations deals with regulatory adaptation designed to preserve the population. From the standpoint of the structure of the system which is modeled, the presence of adaptive characteristics denotes the presence of feedback loops in this structure. The most suitable modeling method which theoretically allows for an unlimited complexity of the model structure, is cybernetic modeling (Menshutkin, 1964), in which the population

can be studied as some finite automaton.

It should be noted that all these models, which are set up to solve problems dealing with the dynamics of the number of fish, presuppose that the actual data which are obtained from fishery statistics and special studies set up to study fishery catches (age, size, sex composition of fish, etc.) and also by additional tests and results obtained from specialized experiments (tagging, quantitative count of ova and larvae, characterization of external conditions, etc.) undergo mathematical treatment in one form or another.

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Ichthyology was one of the first fields to encounter the problem of the rational utilization of self-reproductive natural resources. Already at the end of the 19th century it was noted that the percentage of certain types of fish (sturgeon, giant sturgeon, Caspian sturgeon, sterlet, pike-perch, carp, carp-bream, Caspian roach) in the catches reduced steadily every year. For ichthyologists this fact served as a stimulus to develop the fishing rules (1897) which became the scientific basis for the use of fish reserves.

In 1918 F. I. Baranov built a model which described the dynamic number of fish in stock by assuming that the rate at which the number of fish is reduced with age is proportional to their number. Using a linear relation to describe the relation between age and the length of the fish $l = t$, and a cubic relation for the relation between the weight and the length $p = wl^3$, he obtained the following expression for the ichthyomass of the fishery stock:

$$p(L, k) = wN_0\Omega(L, k),$$

where L is the initial fishery dimension of the fish, N_0 is the recruitment, k is the general mortality coefficient, w is the proportionality coefficient, and $\Omega(L, k)$ is a function which depends on the catches.

$$\Omega(L, k) = \int_L^{\infty} e^{-kl^3} dl.$$

Representing the general mortality coefficient as the sum of the natural and fishery mortality coefficients, Baranov determined the size of the catch and was able to formulate the optimum catch problem. The Baranov model was improved and made more precise in the work of Ricker (Ricker, 1958), Beverton and Holt (Beverton and Holt, 1957), Tanaka (Tanaka, 1957, 1960) and others. Beverton and Holt made a study of the dependence of the catch, the ichthyomass and other population parameters on the fishing rate, the limiting age of fish in the population, the natural mortality and growth parameters.

Thompson (Thompson, 1937), who studied the halibut in the Pacific Ocean, built a stable fishery model. He showed by computations, that as the catching rate increases, the weight of the catch first increases, and then having reached a maximum begins to drop, i.e., Thompson reached the same conclusion about the optimum catch as Baranov, without using the apparatus of differential equations.

The analog modeling experiment of the dynamics of fish populations carried out by Doi (Doi, 1959, 1962) which uses electrodynamic models is interesting. Having noticed the analogy between the differential equations for the dynamics of populations and the processes which take place in electrical circuits, Doi used them as the models for population studies. The possibilities of analog modeling are not confined only to systems which describe processes in electric circuits (networks). Modern analog computers can be used to model rather complex systems of differential equations which do not have analytic solutions in general form. Having at his disposal for the initial data a function of the fishery effort which was determined statistically, Doi determined the population sizes of the Antarctic Finner and King Crab near the shores of Western Kamchatka on an analog computer. These results were used to forecast the fate of these populations given the existing fishing rate. /16

The ideas of Baranov with respect to an optimum catch are developed to some extent in the work of Hjort (Hjort, 1930, 1932, 1933), Russel (Russel, 1931), Gauze (Gauze, 1938). While in all models considered above, the utility function for the population was the catch, M. B. Shefer (Shefer, 1958) introduced as the utility function the revenue obtained from fishing as a branch of the national economy.

4. Optimum Control Models of Biological Associations

Above we considered several types of models in which the problem of acting optimally on the population was posed. We note that the often-used term "control of the population size" is not altogether correct. In fact, no populations can be considered apart from the surrounding biotic and abiotic environment. Even in the simplest population models this effect is always taken into account (by parameters, additional terms in equations, etc.). But the environment is determined by the type of BGC that includes the population under consideration. Therefore, it seems more natural to speak about "controlled action on the BGC" where one of the essential variables is the size of the corresponding population. Nevertheless here, in the literature survey, and in a certain context below, we will use the former term in order not to violate a certain standard presentation.

From the applied standpoint all control models of the population size can be classified into two groups: the control of natural and artificial population sizes.

By control in natural populations we mean intervention in real existing BGC, by control in artificial populations we shall mean a change in the population size and the stock composition by age, the optimal planting planning of seeds, the optimal operating conditions of microorganism cultivators, etc.

A sufficiently large number of studies deal with problems in the second group (Leslie, 1945, 1948; von Foerster, 1959; Spicer, 1955; Yelizarov, Svirezhev, 1967, 1968; Ginzburg, 1968). This is very natural, since the problems themselves are simpler, which is apparently related to the simplicity of the trophic relations and the possibility of determining sufficiently accurately the model parameters.

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The optimality criterion in all these problems is usually related to economic characteristics such as cost (from our point of view), biological productivity of one species or another, or characteristics related to the place which the biosystem under consideration occupies in the general structure of the national economy.

The biological characteristics of the system itself determine the constraints which are imposed on the solution of the problem. The problems of controlling natural populations (intervention in BGC) can be subdivided into utilization problems and suppression problems.

In the first case, which we will mainly study, a part of the biomass of a particular species is removed from the BGC and the biomass removed must have maximum value (again from our point of view).

In the second case our problem consists of changing the trophic and other BGC structures so that the number of "harmful" species will be kept at the lowest possible level (pest control, use of insecticides, etc.).

Often the elementary unit on which we act is the population when the BGC is the elementary unit of the biosphere. It is obvious that control of the number of individuals of one or several species by one or several variables is far from optimal in a system as complex as a BGC. Therefore, we pose the problem of acting optimally on the entire BGC system even in the case when individuals of one or two species from the entire set of species making up the BGC are of economic value.

5. The Simplest Models of Biogeocoenoses

Naturally, before we can formulate the problem of acting optimally on the BGC we must have a model of this system.

In biogeocoenology the number of results, observations and experiments which were accumulated until now is sufficiently large. There is also a considerable number of well established special laws for the development of BGC. However, because of the complexity of studying the many interrelations and interdependences, the general state of biogeocoenotic theory is not yet on a sufficiently high level to permit the effective solution of the problem of long-term forecasting of population sizes, or the problem of optimizing the techniques used in the exploitation of natural arable land. Nevertheless, rather simple BGC models that reflect certain characteristic features of this large system make it possible to formulate for these optimal planning and optimal "yield" problems (in the wide sense) and solve them. /18

We should hardly expect the results obtained in this way to be suitable for working out a concrete plan for the utilization of concrete BGC. However, the qualitative laws which are obtained by solving these problems help us, in the first place, to organize correctly the utilization of natural resources, and, second, enable us, in turn, to construct more realistic BGC models.

The basis which we used in our book are the quantitative models of biological associations which were proposed by V. Volterra. We can say that they are one of the many possible BGC models. An important objection to this point of view is an objection which is related to the dimensionality of the problem. In reality real BGC have hundreds of species, which in turn, are subdivided into groups which differ from one another (by age, size, etc.). If we take for the phase variables only the number of these groups, the dynamic system which describes the BGC will be horrendous. But luckily, the BGC structure is always hierarchial and the structure of the BGC as a whole is determined by one or several species which are called dominant. The dynamics of their size determines the dynamics of the other species. Therefore, for the phase variables in BGC models we can take the size of one, two or several dominant species (these species can include besides the dominant species other species which interest us for other reasons). The interaction with the remaining species and the surrounding non-living nature, can be studied as the interaction with the environment which was subdivided into the biotic and abiotic parts.

Often we cannot say exactly which species are truly dominant. In such a case the choice is entirely up to the investigator.

Since biological systems are usually very large, and the amount of control which any regulator can exert is always limited, the

biologist or engineer must make a choice as to which parameters of the system he can ignore and which he must control (Ashby, 1959, page 12).

So far we used very little the BGC definition in setting up models. But as soon as we pass on to the description of the interaction of the dominant types with the environment (in the Volterra models the description of the parameters), we use the BGC definition in an essential manner. First the parameters of the model represent the averaged characteristics of various interactions, and the average only reflects reality when it is obtained over a sensibly and correctly selected set. The isolation boundaries which exist in reality and a certain degree of homogeneity enable us to consider the BGC as the suitable set for the averaging. Second the stability and the permanent BGC composition which are observed in nature, give reason to hope that these averaged quantities depend very little or not at all on time. All this enables us to consider the BGC as a dynamic system which is described by the equations proposed by Volterra.

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6. Formulation of Basic Concepts and Certain Definitions

By a biogeocoenosis model we will mean a system of $n = r + s$ differential or differential-difference equations with the corresponding constraints on the variables or on their derivatives with respect to time. Here r is the number of different species described in the biogeocoenosis, or if the populations of these species are further subdivided into certain groups (by age, sex, etc.) the number of these groups. The r variables of the system will be either the number of individuals in each group, or the biomass of each group or the density of individuals (provided the individuals are uniformly distributed in space). If it is necessary to take into account the dynamics in the change of environmental factors, this process is described by the remaining s equations of the system. If the environment is constant, $s = 0$. In this case we will often talk about the model and the "biogeocoenosis," meaning by this the biogeocoenosis which goes with the given BGC. Such a model consisting of n equations will be called an n -component BGC model. As we go on we will often omit the word "model" and talk about a n -component BGC, even though in all cases we are talking about the model and not the BGC itself.

Naturally from the standpoint of our formalism models with $n = 1$ and $n = 2$ must exist, i.e. one- and two-component models which we will refer to as one- and two-component BGC. In addition to this we will consider various models of these one- and two-component systems. From this standpoint when we talk in the book about a one- or two-component BGC we do not mean at all that the entire BGC consists of one or two species. We simply study in our model these species by relating the interaction with other species and the interaction between other species to factors in the

biotic environment, which are averaged and described by the parameters of an equation or system.

When $n = 1$ (one-component BGC) the biosystem consists of the population and the environment in which this population lives. We note that when $n = 1$ we cannot speak about biocoenosis, since the concept of an association presupposes the existence of at least two elements of this association. However, the BGC concept which includes the interaction with the environment, allows us to study formally also one-component systems.

When $n = 2$ (two-component BGC) the system consists of two species and the environment. Since the components represent biological species, in this case we can talk about the model of the simplest biocoenosis. These two species may compete with one another, or one species can serve as the food for the other species. In the latter case, we shall talk about biocoenosis or biogeoenosis of the "predator-prey" type. /20

We emphasize once more that in order to avoid confusion whenever we speak about biocoenoses or biogeocoenoses, we only speak about certain models of these which have been simplified to a maximum degree and formalized. These simplest models that we will again call purely formally, one- and two-component BGC, are those building blocks from which more complex models which describe more realistically large systems such as a biogeonosis can be built.

By yield collection we shall mean a certain part of the biomass that was removed from the BGC (a certain number of individuals) of one type of species or another which make up the BGC. The yield collection is considered as a discrete process, i.e., the collecting procedure takes place at certain discrete instants of time by selecting (decantation, catching, shooting) a part of the biomass of the species or groups which make up the BGC.

Since not all species that make up the BGC have the same commercial value, it is natural to assign a certain cost to one unit of the biomass (one individual) in each species or group. By doing this we take into account the economic factors which occur during the utilization of the given BGC.

Chap. II. OPTIMAL POPULATION PRODUCTIVITY

By optimal population productivity we will mean the amount of biomass (or the number of individuals), which was obtained as a result of collecting optimally the yield in a system consisting of a one-species population and its surrounding environment (both abiotic and biotic).

When we formulate and solve optimization problems we will only use deterministic models. This is fully justified if we assume

that the size of the population used is sufficiently large.

In this chapter we will mainly consider two problems. The first problem is the problem of the optimal productivity of a population in a stationary environment. The second problem is formulated for a population model in which the state of the environment (the concentration of the food substance and the rate at which it is supplied) depends essentially on the population size. An example of such a system is an artificial biosystem, the chemostat.

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1. The Problem of Optimizing the Yield Collected from A Homogeneous Population Described by the Volterra Model

We will consider a population consisting of several organisms whose size is bounded above by some limiting factor (limited distribution area, limited amount of food, etc.). In this case the dynamics of the population size are described by an equation of the form (Volterra, 1931):

$$\frac{dN}{dt} = (\alpha - \gamma N)N, \quad (1)$$

where N is the number of individuals in the population at the instant t , α is the natural growth coefficient for the number of individuals in the population, γ is a coefficient which takes into account the competition within the population (for space, food, etc.), where the coefficients $\alpha, \gamma > 0$.

If we denote by N_0 the initial number of individuals in the population, then for any instant of time we have

$$N = \frac{\alpha N_0 e^{\alpha t}}{\alpha + \gamma N_0 (e^{\alpha t} - 1)}. \quad (2)$$

It is easy to see that

$$\lim_{t \rightarrow \infty} N = \frac{\alpha}{\gamma}.$$

Geometrically the solution of equation (1) is described by the logistic curve (see Fig. 1).

Suppose that in the given system the yield is collected by selecting a part of the biomass and by removing it from the reproductive cycle. The process of collecting the yield is assumed to be discrete over time with equal time intervals.

We formulate the problem of controlling optimally the given biomass production system, i.e., the problem of determining the amount of biomass collected in one step and the stepsize between two successive collections with the requirement that the total yield collected over a fixed time interval $[0, T]$, be a maximum. The process terminates at the final instant of time T when the biomass has been fully collected (Yelizarov, Svirezhev, 1967a). The time interval $[0, T]$ is broken up into n equal subintervals by the points $t_i = h, 2h, \dots, nh = T$ and at each step the amount of yield which was collected is defined as

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$$g_i = k_i N_i^-, \quad i = 1, 2, \dots, n,$$

where the index $(-)$ denotes the state of the system at the instant when the yield is collected to the left of t_i and the index $(+)$ when it is collected to the right of t_i . The relation

$$N_{i+1}^+ = N_i^-(1 - k_i), \quad (3)$$

holds, where the quantities $k_i \in [0, 1]$, which are selected at each step are considered as the possible control decisions, which determine for the given state of the system $\{N_i^-\}$, the amount of the yield which was collected.

Following Bellman (Bellman, 1960), we will consider the yield collection process as a multistage decision process with a return function $f_i(N)$ which is equal to the yield collected after i stages with the condition that optimum decisions were used in previous stages.

Using the invariant imbedding method, we can write the recurrence relation for the return function:

$$\begin{aligned} f_1(N) &= \max_{0 \leq k \leq 1} \{kN\}, \\ f_i(N) &= \max_{0 \leq k \leq 1} \{kN + f_{i-1}[P((1-k)N)]\}, \end{aligned} \quad (4)$$

where $N = N_1^-$ is the initial value of the state variable.

For the initial state N we will have for the one-stage process

$$f_1(N) = N, \quad k = 1.$$

Then, in view of (3) and (4), and the principle of optimality

$$f_2(N) = \max_{0 \leq k \leq 1} \left\{ kN + \frac{\alpha(1-k)Ne^{\alpha(t_2-t_1)}}{\alpha + \gamma(1-k)N[e^{\alpha(t_2-t_1)} - 1]} \right\}. \quad (5)$$

Let us introduce the notation $\lambda = e^{\alpha h} = e^{\alpha(t_2-t_1)}$ and $\delta = 1 - k$. It can be shown that the maximum of $f_2(N)$ over δ is obtained when

$$\delta = \frac{\alpha}{\gamma N(\sqrt{\lambda} + 1)},$$

so that the decision in the second stage is

$$k = 1 - \frac{\alpha}{\gamma N(\sqrt{\lambda} + 1)}. \quad (6)$$

Substituting the value obtained in equation (5), we obtain the maximum return from the two-stage optimization process:

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$$f_2(N) = \begin{cases} N + \frac{\alpha}{\gamma} \cdot \frac{\sqrt{\lambda} - 1}{\sqrt{\lambda} + 1}, & \text{when } N > \frac{\alpha}{\gamma(\sqrt{\lambda} + 1)}, \quad k \neq 0 \\ \frac{\alpha \lambda N}{\alpha + \gamma N(\lambda - 1)}, & \text{when } N \leq \frac{\alpha}{\gamma(\sqrt{\lambda} + 1)}, \quad k \equiv 0. \end{cases}$$

Analogously we find the maximum return from the three-stage optimization process and the corresponding decision:

$$f_3(N) = \begin{cases} N + \frac{2\alpha}{\gamma} \cdot \frac{\sqrt{\lambda} - 1}{\sqrt{\lambda} + 1}, & \text{when } N > \frac{\alpha}{\gamma(\sqrt{\lambda} + 1)}, \quad k \neq 0 \\ \frac{\alpha \lambda N}{\alpha + \gamma N(\lambda - 1)} + \frac{\alpha}{\gamma} \cdot \frac{\sqrt{\lambda} - 1}{\sqrt{\lambda} + 1}, & \text{when } N \leq \frac{\alpha}{\gamma(\sqrt{\lambda} + 1)}, \quad k \equiv 0. \end{cases}$$

It is easily seen that if over all stages the value of the state variable satisfies the condition

$$N > \frac{\alpha}{\gamma(\sqrt{\lambda} + 1)}, \quad (7)$$

the corresponding optimal decisions are not zero

$$k = 1 - \frac{\alpha}{\gamma N (\sqrt{\lambda} + 1)} \neq 0$$

and the value of the return function after n stages of the yield collection process is equal to

$$f_n(N) = N + \frac{(n-1)\alpha}{\gamma} \cdot \frac{\sqrt{\lambda}-1}{\sqrt{\lambda}+1}, \quad (8)$$

where

$$N = \frac{\alpha N_0 e^{\alpha h}}{\alpha + \gamma N_0 (e^{2h} - 1)}.$$

Taking into account that $\lambda = e^{2h}$, $h = \frac{T}{n}$ and $n-1 = \frac{T-h}{h}$, we rewrite equality (8) in the form

$$f_n(N) = \frac{\alpha N_0 e^{\alpha h}}{\alpha + \gamma N_0 (e^{2h} - 1)} + \frac{T-h}{h} \cdot \frac{\alpha}{\gamma} \cdot \frac{e^{\frac{\alpha h}{2}} - 1}{e^{\frac{\alpha h}{2}} + 1}. \quad (9)$$

We will clarify the behavior of the return function (9) when the step size h is varied. Since (9) is defined only for $h \geq 0$ it can be shown that the maximum of $f_n(N)$ over h is attained in the limit when $h \rightarrow 0$, regardless of the values of α , γ and N_0 .

Consequently the return function attains the maximum value when the yield is collected continuously, and this maximum is defined as

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$$\lim_{h \rightarrow 0} \left[\frac{\alpha N_0 e^{\alpha h}}{\alpha + \gamma N_0 (e^{2h} - 1)} + \frac{T-h}{h} \cdot \frac{\alpha}{\gamma} \cdot \frac{e^{\frac{\alpha h}{2}} - 1}{e^{\frac{\alpha h}{2}} + 1} \right] = N_0 + \frac{\alpha^2 T}{4\gamma}. \quad (10)$$

Since it is assumed that the decision is not zero over all stages, its value is defined as

$$\lim_{h \rightarrow 0} \left[1 - \frac{\alpha}{\gamma N \left(e^{\frac{\alpha h}{2}} + 1 \right)} \right] = 1 - \frac{\alpha}{2\gamma N}$$

and the bound $N > \frac{\alpha}{2\gamma}$ must be satisfied. This inequality enables us to determine the optimal initial conditions when the yield is collected continuously.

We will consider the case when condition (7) is not satisfied in a certain stage. We will show that if condition (7) is satisfied in the i -th stage, it will also be satisfied in any j -th stage where $j > i$ (when the decisions in the successive stages are selected optimally). Thus, if

$$N_i^- > \frac{\alpha}{\gamma \left(e^{\frac{\alpha h}{2}} + 1 \right)},$$

$$k_i = 1 - \frac{\alpha}{\gamma N_i^- \left(e^{\frac{\alpha h}{2}} + 1 \right)}.$$

Then, according to (3),

$$N_{i+1}^+ = \frac{\alpha}{\gamma N_i^- \left(e^{\frac{\alpha h}{2}} + 1 \right)} \cdot N_i^- = \frac{\alpha}{\gamma \left(e^{\frac{\alpha h}{2}} + 1 \right)}.$$

Consequently

$$N_{i+1}^- = \frac{\alpha}{\gamma \left(e^{\frac{\alpha h}{2}} + 1 \right)} \cdot e^{\frac{\alpha h}{2}}.$$

It is easily seen that

$$N_{i+1}^- \geq N_i^- > \frac{\alpha}{\gamma \left(e^{\frac{\alpha h}{2}} + 1 \right)},$$

hence $k_{i+1} \neq 0$.

Therefore, condition (7) may not be satisfied only in some J initial stages of the process. Then in these J stages the decision

must be zero ($k \equiv 0$), until in the $(J+1)$ -th stage condition (7) is satisfied. The number J depends on the N_0 and h selected and /25
it is defined as

$$J = E\left(\frac{\Delta T}{h}\right) + 1,$$

where $E(x)$ is the integer part of the number x , and ΔT is a root of the equation

$$\frac{\alpha}{\gamma\left(e^{\frac{\alpha h}{\gamma}} + 1\right)} = \frac{\alpha N_0 e^{\alpha \Delta T}}{\alpha + \gamma N_0 (e^{\alpha \Delta T} - 1)}.$$

The return function is equal to

$$f_n(N) = \frac{\alpha N_0 e^{\alpha \Delta T}}{\alpha + \gamma N_0 (e^{\alpha \Delta T} - 1)} + \frac{(n - J - 1)\alpha}{\gamma} \cdot \frac{e^{\frac{\alpha h}{\gamma}} - 1}{e^{\frac{\alpha h}{\gamma}} + 1},$$

where in the first J stages of the process $k \equiv 0$, and in the remaining $n - J$ stages the decision is defined by expression (6). This means that when the number of organisms in the population is below a certain level defined by inequality (7), we must not collect the yield at all, and only when this level is reached the subsequent collections are different from zero. We note that the total yield depends on the stepsize used in the process, and is a maximum when the collection is continuous.

2. Algorithm for the Numerical Solution for the Optimal Yield Collection Problem in a Homogeneous Population

In the case when the coefficients in equation (1) are functions of time or some other parameters of the process, it is not possible to obtain an analytic solution of the problem and the problem must be solved numerically. We will construct an algorithm for the numerical solution of the problem, assuming that the coefficients in (1) are known functions of time given in the form of a table.

The number of individuals in the population will be called the state variable, and we introduce the concept of a scale of states (Moiseyev, 1965). To do this we will consider the space (N, t) and

we will specify the step h over time. We will consider in the hyperplanes $t_i = ih$ the finite sets $\{N_i^s\}$, the sets of nodes of a grid ($i=1,2,\dots,n$; $s=1,2,\dots,m$) where i is the number of the step over time and s is the number of the level of the state variable.

At discrete instants of time $t_i = ih$, we act on the system by selecting a part of the biomass from the population and removing it from the reproductive cycle. The biomass which was removed from the population is considered as the yield. We formulate the problem of maximizing the yield collected in n steps

$$G = \sum_{i=1}^n k_i N_i,$$

where N_i is the value of the state variable at the instant t_i , and $k_i \in [0, 1]$ are quantities which determine the admissible decisions at the same instant of time. /26

The numerical solution of the problem of maximizing the yield collected in the system under consideration will be executed on an electronic digital computer using the following algorithm.

We construct a grid of nodes for the change of state of the state variable $\{N^s(0)\}$.

Remark 1

1) Generally $\{N^s(0)\}$ may also depend on the number of the level over time.

2) We introduce the quantities G_i^s (G_i^s is the maximum yield in i steps for the s -th node of the state variable). For the given node at the initial instant of time we let $G_0^{s_{data}} = 0$, and for the remaining nodes $G_0^s = -1$ ($s \neq s_{data}$). A total negative yield for the s -th node denotes that the state variable cannot arrive to this node.

3) For the admissible values of the state variable in the $(i-1)$ -st level over time ($G_{i-1}^s \geq 0$), by integrating numerically (1) we calculate the values $N_s(h)$ of the state variable at the end of the i -th step, and for all nodes ($\gamma = 1, 2, \dots, m$) of the next i -th level we calculate over time the value of the yield at the step that can be obtained when the state variable makes the transition from the s -th into the j -th node.

$$D_s^i = N_s(h) - N^i(0).$$

If the state variable cannot leave the s-th node ($G_{i-1}^s < 0$) or if it cannot arrive at the j-th node ($D_s^j < 0$) we set

$$D_s^j = -1.$$

4) Using Bellman's optimality principle for all possible ($D_s^j \geq 0$) transitions from the (i-1)-th level into the i-th level over time, we find the maximum total yield over all nodes of the (i-1)-st level after i steps

$$G_{\max}^i = G_{i-1}^{s_{\max}} + D_{s_{\max}}^i,$$

where s_{\max} is the number of the node in the (i-1)-th level over time which yields the maximum yield in i steps.

5) Using the formula

$$k^i = \frac{D_{s_{\max}}^i}{D_{s_{\max}}^i + N^i(0)}$$

we calculate the optimal decisions in the i-th level over time for the arrival of the state variable in the j-th node, and if such transition is not possible, we set $k^j = -1$, which allows us to ignore in the analysis of the computational results the corresponding path of the state variable. /27

6) The optimal values of the total yield which were found are printed out and are used to continue the calculations in the next step over time.

7) Printing out at each step over time the arrays k^j , D_{\max}^j , G_{\max}^j , $N^j(0)$ ($j = 1, 2, \dots, m$) and analyzing the results that were obtained, we can easily determine the optimum path of the state variable, the optimal policy and the maximum yield collected in $i = 1, 2, \dots, n$ steps.

Remark 2

Let us assume that we found a path N^* , a decision k^* and the value of the total yield G^* along this path. We can always improve the accuracy of this solution by reducing the step over time and constructing in the neighborhood of N^* a new scale of states with a smaller step for the variable N , and by constructing the new scale of states in such a way that the points of the old scale are among the points of the new scale. As a result we obtain a new solution, the curve N^{**} , the decision k^{**} and the value of the total yield G^{**} . Since the curve N^* was among the admissible optimization paths, $G^{**} \geq G^*$.

The process which was described can be repeated an infinite number of times. As a result we obtain a sequence of values of the total yield $G^* \leq G^{**} \leq G^{***} \leq \dots$ and a sequence of decisions $\{k^{n*}\}$. Since the value of the total yield is bounded above (10), the sequence $\{G^{n*}\}$ converges.

Unfortunately, until now the problem of the dependence of the limiting values of the unknown quantities on the steps in the phase and time variables when the iterative process is continued indefinitely has not yet been worked out.

When we make the calculations we will use the following technique (Moiseyev, 1965). We fix the step size over time and in each stage of the iterative process we will break up the step only over the phase variable (state variable). After we obtain the "limiting value" for the given partition of the time axis, we will reduce the step over time, and repeat the whole procedure, etc.

We give the algorithm which was described above for the numerical solution of the problem of optimizing the yield collected in a homogeneous population, which is described by the Volterra model in the form of a program (Program 1), written in the ALGOL-60 algorithmic language (Ageyev, 1965).

Program 1

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```
begin integer i, j, m, n, sdata, Nint, NINT;
  real Ns, Ndown, Nup, T, alfa, gamma;
  array N, Sn, ax, Gmax, Dmax, k, G [1 : m], NS, y [1 : 1],
  D [1 : m, 1 : m], B [0 : 2, 1 : NINT];
  procedure inter (n, x, y);
    value n, x; integer n; real x, y;
  begin
    L: if x >= B [0, Nint] then
      begin
        L1: if x < B [0, Nint - 1] then
          begin y := (B [n, Nint] * (x - B [0, Nint - 1]) +
            B [n, Nint - 1] * (B [0, Nint] - x)) /
            (B [0, Nint] - B [0, Nint - 1]); go to L2
          end else Nint := Nint + 1;
            if Nint > NINT then stop; go to L1
          end else Nint := Nint - 1; if Nint < 1 then stop;
            go to L
        end
      end
```

```

L2: end;
procedure f (x, y, r, z);
  value x, y, r; real x; integer r; array y, z;
  begin inter (1, x, alfa); inter (2, x, gamma);
    z := (alfa - gamma × y [1]) × y [1]
  end;
procedure runge (x, y, r, f, eps, eta, prim, xfin) result: (yfin);
  value x, y; real x, eps, eta, xfin; integer r;
  Boolean prim; array y, yfin; procedure f;
  begin real x1, x2, x3, h; integer k, j; Boolean out;
    array z, y1, y2, y3 [1 : r];
    procedure rk1step (x, y, h) result: (xh, yh);
      real x, h, xh; array y, yh;
      begin integer j, k; array z, w [1 : r], a [1 : 5];
        a [1] := a [2] := a [5] := 5 × h;
        a [3] := a [4] := h; xh := x;
        for k := 1 step 1 until r do
          yh [k] := w [k] := y [k];
          for j := 1, 2, 3, 4 do
            begin f (xh, w, r, z);
              xh := x + a [j];
              for k := 1 step 1 until r do
                begin yh [k] := yh [k] + a [j + 1] × z [k] / 3;
                  w [k] := y [k] + a [j] × z [k]
                end k
              end j
            end rk1step
          if prim then begin h := xfin - x; ss := 0
            end else h := hs;
          out := false;
          lab1: if (x + 2.01 × h - xfin > 0) ≡ (h > 0) then
            begin hs := h; out := true;
              h := (xfin - x) / 2
            end;
          rk1step (x, y, 2h, x1, y1);
          lab2: rk1step (x, y, h, x2, y2);
            rk1step (x2, y2, h, x3, y3);
            for k := 1 step 1 until r do
              if comp (y1 [k], y3 [k], eta) > eps then
                go to lab3;
              x := x3;
              if out then go to fin;
              for k := 1 step 1 until r do y [k] := y3 [k];
              if ss = 5 then begin ss := 0; h := 2 × h end;
              ss := ss + 1; go to lab1;
            lab3: h := 0.5 × h; out := false; x1 := x2;
              for k := 1 step 1 until r do y1 [k] := y2 [k];
              go to lab2;
            fin: for k := 1 step 1 until r do yfin [k] := y3 [k]
          end runge;
          Comment Here we use the standard Runge-Kutta procedure
            (Ageev, Alik, Galis, 1966)
            N1ht := 1;
            for s := 1 step 1 until m do
              begin N [s] := (Nup - Ndown) × (s - 1) / (m - 1); G [s] := -1.0
            end; G [sdata] := 0.0;
            Comment The scale of states was set up and the calculations
              were initialized
            for i := 1 step 1 until n do
              begin for s := 1 step 1 until m do
                begin if G [s] < 0 then
                  begin for j := 1 step 1 until m do D [s, j] := -1
                end else
                  begin y [1] := N [s]; runge (0, y, 1, f, eps, eta,
                    true, T / n, NS); NS := NS [1];
                    for j := 1 step 1 until m do
                      if NS < N [j] then D [s, j] := -1.0 else
                        D [s, j] := NS - N [j]
                    end
                  end
                end
              end
            end

```



```

end;
begin
  for j:=1 step 1 until m do
    Smax [j]:=0; Gmax [j]:=-1.0; Dmax [j]:=0;
    for s:=1 step 1 until m do
      begin if D [s, j] >= 0 then
        begin if Gmax [j] < G [s] + D [s, j] then
          begin Gmax [j]:=G [s] + D [s, j];
            Smax [j]:=s; Dmax [j]:=D [s, j]
          end
        end
      end
    end
  end;
  for j:=1 step 1 until m do
    begin if Dmax [j] > 0 then
      k [j]:=Dmax [j] / (Dmax [j] + N [j])
    else k [j]:=-1.0; G[j]:=Gmax [j]
    end;
    print (j, k, N, Dmax, Gmax)
  end i
end program.

```

We give a computational example for a concrete problem calculated using the algorithm which was constructed. For simplicity we let:

$$\begin{aligned}
 \alpha &= 1 \text{ [1/hr]}, & \gamma &= 10^{-6} \text{ [ml/hr]}, \\
 N_0 &= 0.54 \cdot 10^6 \text{ [1/ml]}, & T &= 500 \text{ hr}
 \end{aligned}$$

The results of the numerical solution of the dependence of the total yield on the step size are given below.

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| Step size, hr | 0 | 1 | 2 | 5 | 10 | 20 | 50 | 100 | 500 |
|---|------|--------|--------|--------|--------|--------|-------|-------|-----|
| Total yield in 500 hr, in millions of units/ml | 13.0 | 12.996 | 12.992 | 12.894 | 12.583 | 11.360 | 9.331 | 5.434 | 1.0 |

Many computations on the electronic digital computer have shown that when the yield is collected optimally, the collection process becomes quickly stationary. Initial conditions exist for which the process becomes stationary at the first step. It is important that the total yield depends on the step in the process and tends to a maximum as $h \rightarrow 0$.

3. Population of Microorganisms in a Chemostat

An example of a device which can be used to preserve indefinitely a population of bacteria in an active state and control its development is a chemostat (Fig. 3), an apparatus which was designed for the continuous cultivation of microorganisms (Novick, Szilard, 1950). This apparatus automatically reproduces the nutrient environment in the vessel in which the bacteria are grown, which facilitates the growth of the microorganisms, and at the

same time mixes the particles of this suspension

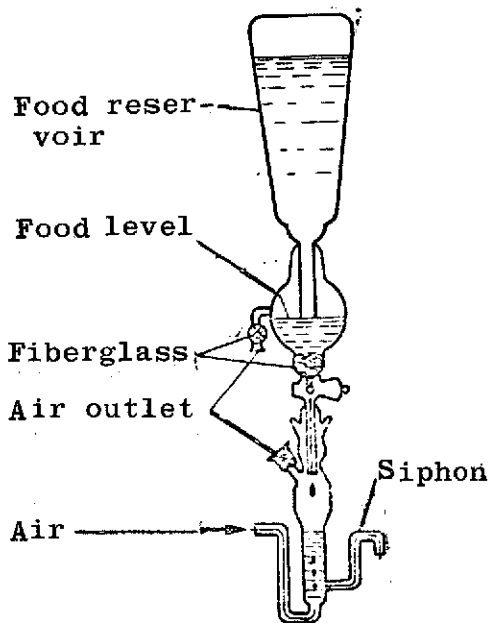


Fig. 3. Chemostat Device

Sterilized and chemically pure liquid food is transferred at a constant rate from a storage tank into the vessel with the culture. This type of supply maintains the same level of liquid in the vessel, and consequently preserves the constant suspension volume. The bacterial suspension is poured out from the vessel at the same rate at which new food arrives in the vessel. The culture is stirred sufficiently well in the vessel so that the food which arrives there is quickly and uniformly distributed in the vessel. Every particle of the culture can be removed with a certain probability from the vessel within a certain time interval.

Therefore, if we denote by N the concentration of certain particles or organisms, by w the magnitude of the suspension flow through the siphon (see Fig. 3) per unit time and by v the volume of the culture,

then the rate at which the particles are ejected from the vessel with the culture is defined as

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$$\frac{dN}{dt} = - (w/v) N = - \omega N.$$

The quantity ω is called the "dilution rate." It is usually constant.

In a chemostat the bacterial synthesis process is controlled by one limiting growth factor (LGF) which induces a metabolism which depends only on this factor.

If C is the LGF concentration in the culture, then on the basis of the data of Spicer (Spicer, 1955) the synthetic activity of a bacterial population of density N is characterized by the rate

$$\frac{dN}{dt} = \lambda C N,$$

where λ is the proportionality coefficient.

On the basis of experimental data (Monod, 1942, 1949; Novick, Szilard, 1950) it was shown that the LGF used up during the population growth is proportional to the rate of growth for a certain concentration C

$$\frac{dC}{dt} = -q \frac{dN}{dt} = -q\lambda CN.$$

The proportionality coefficient q is measured by the amount of LGF used up by the bacteria and it is called the "assimilation rate constant."

When the concentration of LGF in the food which is supplied is a , and a homogeneous population of density N is grown in the vessel with the culture, the rate of change of the LGF concentration in the culture in the chemostat is

$$\frac{dC}{dt} = \omega(a - C) - \lambda q CN.$$

Consequently the growth dynamics of the bacterial population in the chemostat can be described by the following mathematical model (Moser, 1957):

$$\left. \begin{aligned} \frac{dN}{dt} &= (\lambda C - \omega) N \\ \frac{dC}{dt} &= \omega(a - C) - \lambda q CN \end{aligned} \right\} \quad (11)$$

Figure 4 shows the graphs which describe the dynamics of the change in the LGF concentration and the microorganism density N for the *Escherichia coli* B population in the chemostat. It is easily seen that N and C tend over time to stationary values which are defined as

$$\tilde{C} = \frac{\omega}{\lambda}, \quad \tilde{N} = \frac{a - \tilde{C}}{q}. \quad (12)$$

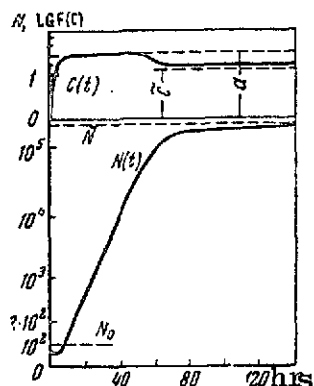


Fig. 4. Change in the concentration of the limiting growth factor (C) and the density (N) of the *Escherichia coli* B microorganism in the chemostat culture ($\lambda = 3.6 \cdot 10^8$ ml/g.hr; $q = 2 \cdot 10^{-15}$ g, $a = 1.5 \cdot 10^{-9}$ g/ml, $\omega = 0.4$ l/hr., $N_0 = 10^2$ l/ml, $C_0 = 0$)

4. Optimal Productivity of a Chemostat

We consider the problem of collecting optimally the yield in a homogeneous population of microorganisms in a chemostat whose growth dynamics are described by the system of differential equations (11) (Yelizarov, Svirezhev, 1967b; Yelizarov, 1968). The yield is collected by pouring off a part of the suspension that contains both the biomass and the nutrient substrates at discrete instants of time t_i ($i = 1, 2, \dots, n$; $h = T/n$; $n = \text{const}$). Only the biomass of the microorganisms has productive value. At each step we remove a certain amount of biomass from the population.

$$g_i = k_i N_i^-$$

The controls are the quantities $k_i \in [0, 1]$. We formulate the problem of maximizing the return function (the value of the total yield

$$f_n(N) = G = \sum_{i=1}^n k_i N_i^-$$

collected over a fixed time interval $[0, T]$).

The first integral of system (11) is:

$$C(t) = a - qN + (C_0 + qN_0 - a) e^{-\omega t}, \quad (13)$$

where N_0 and C_0 are the values of the corresponding variables at the

initial instant of time.

Eliminating the variable C from the first equation in system (11), we obtain the result that the process in the chemostat can be described by the following system of equations which is equivalent to system (11):

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$$\left. \begin{aligned} \frac{dN}{dt} &= [\lambda a - \omega + \lambda(C_0 + qN_0 - a)e^{-\omega t}]N - \lambda qN^2 \\ C(t) &= a - qN + (C_0 + qN_0 - a)e^{-\omega t} \end{aligned} \right\} \quad (14)$$

We note that the quantity

$$\beta = (C_0 + qN_0 - a)e^{-\omega t}$$

in equation (13) decreases monotonically as t increases ($\omega > 0$), so that for sufficiently large t , the solution of system (14) will be close to the solution of a system of the form:

$$\left. \begin{aligned} \frac{dN}{dt} &= (\lambda a - \omega)N - \lambda qN^2 \\ C(t) &= a - qN \end{aligned} \right\} \quad (15)$$

The state described by (15) will be called a quasistationary state of the population. It is easily seen that the first equation in system (15) coincides with the Volterra equation in Section 1 except for the designation of the coefficients. The second equation in the system relates the density of the microorganisms to the concentration of food in the vessel with the culture (an additional constraint on N).

Suppose that the yield collection process begins at the instant when the population is in the quasistationary state. We will show that collecting the yield does not violate quasistationarity of the population, i.e., the quantity β does not increase in the yield collection process. In fact when the yield is collected the relations

$$N_{i+1}^* = N_i^* (1 - k_i), \quad (16)$$

$$C_{i+1}^* = C_i^* + (a - C_i^*)k_i \quad (17)$$

hold. A simple transformation of these relations gives

$$C_{i+1}^+ + qN_{i+1}^- = C_i^- + qN_i^- - (C_i^- + qN_i^- - a)k_i$$

or

$$\beta_{i+1}^+ = \beta_i^-(1 - k_i).$$

Since $k_i \in [0, 1]$, $\beta_{i+1}^+ \leq \beta_i^-$, which was to be shown.

5. Numerical Solution of the Optimal Productivity Problem of the Chemostat

In this case, even when the coefficients in equation (11) are constant, it is not possible to obtain a complete analytic solution for the problem which was formulated. The algorithm for the numerical solution of the problem of optimizing the chemostat productivity is the same as that which was given for the optimization of the yield collected in a homogeneous population. We give the program (Program 2) for the numerical solution of the optimization problem in the general formulation (a , q , λ , ω are known functions of time given in tabular form. The assumption that the yield collection process is quasistationary is not made). /34

Program 2

```
begin integer i, j, s, m, n, sdata, Nint, NINT;
  real Ns, Cs, Nup, Ndown, Cdata, T, a, q, lambda, omega;
  array N, C, Smax, Gmax, Dmax, k, G [1:m], yfin, y [1:2],
  D [1:m, 1:m], B [0:4, 1:NINT];
  Comment: y[1:2] vector with the coordinates N & C
  procedure inter (n, x, y);
    Comment: The interpolation procedure is described
    in Program 1,
```

```

procedure f (x, y, r, z);
  value x, y, r; real x; integer r; array y, z;
  begin
    inter (1, x, a); inter (2, x, q);
    inter (3, x, lambda); inter (4, x, omega);
    z [1] := (lambda × y [2] - omega) × y [1];
    z [2] := (a - y [2]) × omega - lambda × q × y [1] × y [2]
  end;
procedure runge (x, y, r, f, eps, eta, prim, xfin) result: (yfin);
  Comment: The Runge-Kutta procedure is described
            in Program 1,

```

```

      Nint:=1
for s:=1 step 1 until m do
begin N [s] := (Nup - Ndown) × (s - 1)/(m - 1);
  C [s] := Cdata; G [s] := -1.0
end
G [sdata] := 0;
for i:=1 step 1 until n do
begin for s:=1 step 1 until m do
  begin if G [s] < 0 then
    begin for j:=1 step 1 until m do
      D [s, j] := -1.0
    end else
      begin y [1] := N [s]; y [2] := C [s];
        runge (0, y, 2, f, eps, eta, true, T/n, yfin);
        Ns := yfin [1]; Cs := yfin [2];
        for j:=1 step 1 until m do
          if Ns < N [j] then D [s, j] := -1.0 else
            D [s, j] := Ns - N [j]
        end
      end
    end
  end
  for j:=1 step 1 until m do
begin Smax [j] := 0; Gmax [j] := -1.0; Dmax [j] := 0;
  for s:=1 step 1 until m do
begin if D [s, j] ≥ 0 then
  begin if Gmax [j] < G [s] + D [s, j] then
    begin Gmax [j] := G [s] + D [s, j];
      Smax [j] := s; Dmax [j] := D [s, j]
    end
  end
end
end
end;
for j:=1 step 1 until m do
begin if Dmax [j] > 0 then
  k [j] := Dmax [j] / (Dmax [j] + N [j]);
  C [j] := (a - Cs) × k [j] + Cs else
    k [j] := -1.0;
    G [j] := Gmax [j]
  end;
  print (i, k, N, C, Dmax, Gmax)
end i

```

end program

Program 2 was written for an electronic digital computer. The computations have shown that the qualitative picture of the yield collection process in the population cultivated in a chemostat is analogous to the process considered in Section 1. Figure 5 gives the graphs for the change in N and C over time for the optimal yield collection process.

On the basis of a large number of numerical computations we can conclude that the optimal yield collection process in such a system becomes quickly stationary, while the transition time of the process does not exceed the characteristic population time T^* . The characteristic population time is the time it takes the

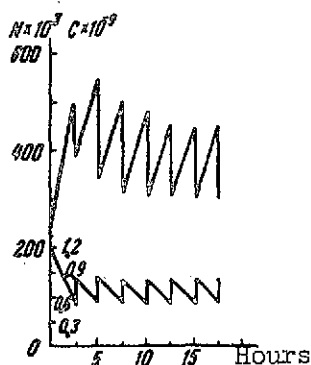


Fig. 5

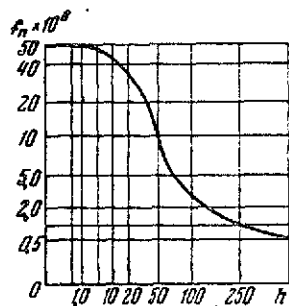


Fig. 6

Fig. 5. Change in the density (N) of the microorganisms and the concentration (C) in the limiting factor during the optimal yield collection process in the chemostat ($N_0 = 260\,000$ l/ml, $C_0 = 1.2 \cdot 10^{-9}$ g/ml, $a = 1.5 \cdot 10^{-9}$ g/ml, $\lambda = 3.6 \cdot 10^8$ ml/g.hr., $\omega = 0.1$ 1/hr, $q = 2 \cdot 10^{-15}$ g)

Fig. 6. The optimal total yield (f_n) versus the step size in the process (h)

population-size to reach a level which is equal to 0.9 of the limit (12):

$$T^* = \frac{1}{\lambda a - \omega} \ln 9 \left(\frac{\lambda a - \omega}{\lambda q N_0} - 1 \right).$$

A study of the relation between the optimal value of the total yield and the step size of the process has shown that this quantity tends to a maximum when $h \rightarrow 0$ (Fig. 6).

6. Total Productivity of the Population Cultivated in the Chemostat

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We will change somewhat the formulation of the problem of optimizing the yield collected in the population cultivated in the chemostat. We define the amount of yield collected at each step as

$$g_i = k_i N_i + \omega \int_{t_{i-1}}^{t_i} N(t) dt.$$

This corresponds to the assumption that the part of microorganisms in the population which is ejected from the chemostat when the suspension is poured through the bottom of the vessel with the culture is included in the total yield. We will consider the problem of collecting the yield with a modified criterion function in the case when at the initial instant of time the population in the chemostat is in a quasistationary state.

$$f_n(N) = \sum_{i=1}^n k_i N_i + \omega \int_0^T N(t) dt$$

The operator P for the transition from states $\{N_1^+\}$ into states $\{N_1^-\}$, or equivalently, the solution of the first equation of system (15) over one step can be written as

$$N(t) = \frac{(\lambda a - \omega) N_0 e^{(\lambda a - \omega)t}}{\lambda a - \omega + \lambda q N_0 [e^{(\lambda a - \omega)t} - 1]}. \quad (18)$$

The recurrence relation for the return function is

$$\begin{aligned} f_1(N) &= \max_{0 \leq k \leq 1} \left\{ kN + \omega \int_0^{t_1} N(t) dt \right\}, \\ f_i(N) &= \max_{0 \leq k \leq 1} \left\{ kN + f_{i-1}[P((1-k)N)] + \omega \int_{t_{i-1}}^{t_i} N(t) dt \right\}, \\ i &= 2, 3, \dots, n. \end{aligned}$$

Integrating (18) over one step we obtain

$$\int_{t_{i-1}}^{t_i} N(t) dt = -\frac{1}{\lambda q} \ln \left[1 - \frac{\lambda q N_i^-}{\lambda a - \omega} (1 - e^{-h(\lambda a - \omega)}) \right]$$

Applying the procedure for finding the optimum decision similarly as in Chapter II, the values of the return function can be written as

a) for the one-stage process:

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$$f_1(N) = N - \frac{\omega}{\lambda q} \ln \left[1 - \frac{\lambda q N}{\lambda a - \omega} (1 - e^{-h(\lambda a - \omega)}) \right].$$

b) for the n-stage process:

$$\begin{aligned} f_n(N) &= N - \frac{\omega}{\lambda q} \ln \left[1 - \frac{\lambda q N}{\lambda a - \omega} (1 - e^{-h(\lambda a - \omega)}) \right] + \\ &+ \frac{(n-1)\omega}{\lambda q} \ln \frac{1}{2} \left[Q + \frac{\omega}{\lambda a - \omega} (e^{h(\lambda a - \omega)} - 1) \right] + \\ &+ \frac{n-1}{\lambda q} \left[\frac{(Q-2)(\lambda a - \omega)}{e^{h(\lambda a - \omega)} - 1} + \omega \right] \left[\frac{e^{h(\lambda a - \omega)}}{Q + \frac{\omega}{\lambda a - \omega} [e^{h(\lambda a - \omega)} - 1]} - \frac{1}{2} \right], \end{aligned}$$

where

$$Q = \sqrt{4e^{h(\lambda a - \omega)} + \left[\frac{\omega}{\lambda a - \omega} (e^{h(\lambda a - \omega)} - 1) \right]^2}.$$

The relation for $f_n(N)$ is valid when

$$N > N^* = \frac{1}{2} \left[\frac{(Q-2)(\lambda\alpha - \omega)}{e^{h(\lambda\alpha - \omega)} - 1} + \omega \right].$$

The decision is different from zero

$$k = 1 - \frac{N^*}{2N} \neq 0$$

and the relation $C(t) = a - qN(t)$ is satisfied.

7. Calculation of the Total Optimal Productivity of the Population Cultivated in the Chemostat

The numerical solution of the problem formulated in Section 6 will be carried out using the following algorithm:

1. We construct a scale of states $\{y^s(0)\}$ where $s = 1, 2, \dots, m$, and $y(0)$ is the density of the microorganisms in the population at the instant when the yield is collected to the right of t_i .

2. We introduce the quantities G_i^s (G_i^s is the maximum yield in i steps for the s -th node of the scale of states). For the given node we set $G_0^{sdata} = 0$ at the initial instant of time, and for the remaining nodes $G_0^s = -1$ ($s \neq data$). A negative value for the total yield for the s -th node indicates that the state variable cannot arrive at this node.

3. For all nodes $\{y^p(0)\}$ ($p = 1, 2, \dots, m$) of the scale of states we calculate by integrating numerically system (11) together with equation

$$\frac{dI}{dt} = \omega N(t)$$

a matrix of values of the state variable N , the LGF concentration in the vessel with the culture C , and the integral

$$J = \omega \int_0^h N(t) dt$$

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over time at the end of the step (before the yield is collected).

4. For all nodes ($j = 1, 2, \dots, m$) of the state variable which can be reached from the s -th nodes ($G_{i-1}^s \geq 0$), we calculate the yield per step (i -th level over time):

$$D_s^j = yj[1, s] - y_s[1, j] + yj[3, s].$$

If the state variable cannot leave the s -th node ($G_{i-1}^s < 0$) or arrive at the j -th node ($D_s^j < 0$), we set

$$D_s^j = -1.$$

5. Using Bellman's optimality principle for all possible transitions ($D_s^j \geq 0$) from the $(i-1)$ -th level to the i -th level over time, we find the maximum total yield after i steps over all nodes in the $(i-1)$ -st level:

$$G_{\max}^i = G_{i-1}^{s_{\max}} + D_{s_{\max}}^j,$$

where s_{\max} is the number of the node in the $(i-1)$ -th level over time which yields the maximum total yield in i -steps.

6. Using the formula

$$k^j = \frac{yj[1, p] - y_s[1, j]}{yj[1, p]},$$

where $p = s_{\max}$, we calculate the optimum decision in the i -th level over time when the state variable is in the j -th node, and when it cannot arrive there we set $k^j = -1$ which allows us to ignore the path of the state variable in the analysis of the computational results.

7. The optimum values of the total yield which were found are printed out and used to continue the calculations at the next step over time.

8. Printing out at each step over time the arrays k , D_{\max}^j , G_{\max}^i , yj , y_s and the values s_{\max} when we analyze the computational

results we determine the optimum path of the state variable, the optimum policy and the maximum total yield collected in $i = 1, 2, \dots, n$ steps.

The algorithm presented above was written for an electronic digital computer in the ALGOL-60 language as the following program (Program 3):

Program 3

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```

begin integer i, j, n, m, p, sdata;
  real Nup, Ndown, Cdata, T, a, q, lambda, omega;
  array yrs [1:3] Smax, Gmax, Dmax, k, G [1:m];
  yjr [1:3], ys [1:3, 1:m], yj [1:3, 1:m], D [1:m, 1:m];
  Comment:ys [1,s] = N[s] - scale of states
           (s = 1, 2, . . . , m),
           ys [2,s] = C[s] - concentration values
           LGF at the nodes of the scale of states

           ys [3,s] = J[s] - the initial value of the
                               integral  $J = \omega \int_{t_{i-1}}^{t_i} N(t)dt;$ 

  procedure f(x, y, r, z);
    value x, y, r; real x; integer r; array y, lz; begin
      z [1] := (lambda × y [2] - omega) × y [1];
      z [2] := (a - y [2]) × omega - lambda × q × y [1] × y [2];
      z [3] := omega × y [1] end;
  procedure runge (x, y, r, f, eps, eta, prim, xfin) result: (yfin);
    Comment:The Runge-Kutta procedure is described in Program 1;
    for s:=1 step 1 until m do
      begin ys [1, s] := (Nup - Ndown) × (s - 1)/(m - 1);
            ys [2, s] := Cdata; ys [3, s] := 0;
            G [s] := -1.0
        end G [sdata] := 0;
    Comment:The scale of states has been constructed and the
              computations have been initialized

    for i:=1 step 1 until n do
      begin for p:=1 step 1 until m do
        begin for i:=1, 2, 3 do yrs [i] := ys [i, p];
              runge (0, yrs, 3, f, eps, eta, true, T/n, yjr);
              for i:=1, 2, 3 do yj [i, p] := yjr [i]
        end;
      end;
    Comment:The values N, C and D at the end of the step
              before the yield is collected have been calculated

```

```

for s:=1 step 1 until m do
begin if G [s] < .0 then
begin for j:=1 step 1 until m do
D [s, j]:=-1.0
end else
for j:=1 step 1 until m do
D[s, j]:= (if yj [1, s] < ys [1, j] then -1.0 else
yj [1, s] - ys [1, j] + yj [3, s]);
end;
for j:=1 step 1 until m do
begin Smax [j]:=0; Gmax [j]:=-1.0; Dmax [j]:=0;
for s:=1 step 1 until m do
begin if D [s, j] ≥ 0 then
begin if Gmax [j] < G [s] + D [s, j] then
begin Gmax [j]:=G [s] + D [s, j];
Smax [j]:=s; Dmax [j]:=D [s, j]
end
end
end
end;
end;
for j:=1 step 1 until m do
begin k [j]:=-1.0; ys [3, j]:=0.0; p:=Smax [j];
G [j]:=Gmax [j];
if Dmax [j] > 0 then
begin k [j]:= (yj [1, p] - ys [1, j]) / (yj [1, p]);
ys [2, j]:= (a - yj[2, p]) × k [j] + yj [2, p];
end
end;
print (i, k, yj, ys, Smax, Dmax, Gmax)
end i
end program.

```

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Computations using the above program have shown that the introduction of an integral term into the criterion function which describes the biomass collection process in the chemostat more realistically, increases only the total amount of the yield which was collected. The qualitative picture of the process is analogous to the picture of the yield collection process in which the criterion function has no integral term (i.e., in the total useful biomass, the biomass which is "washed out" from the chemostat is not taken into account).

As an illustration, Figs. 7 and 8 give the results of the computations on an electronic digital computer for the problem of optimizing the total productivity of the population cultivated in the chemostat

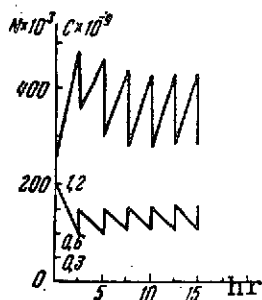


Fig. 7

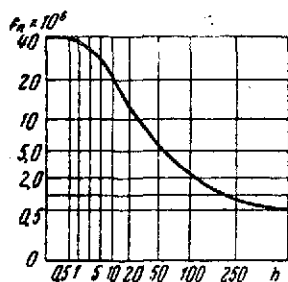


Fig. 8

Fig. 7. Change in N and G for the optimal yield collection process in the general chemostat productivity problem ($N_0 = 260\,000$ l/ml, $C_0 = 1.2 \cdot 10^{-9}$ g/ml, $a = 1.5 \cdot 10^{-9}$ g/ml, $\lambda = 3.6 \cdot 10^8$ ml/g.h, $\omega = 0.1$ l/h, $q = 2 \cdot 10^{-15}$ g)

Fig. 8. Total optimal yield (f_n) versus the step size (h) in the general chemostat productivity problem.

CHAP. III. OPTIMAL PRODUCTIVITY OF A BIOSYSTEM OF THE "PREDATOR-PREY" TYPE

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1. Description of the Mathematical Model

We will consider a Volterra biocoenosis model (a mathematical model for two coexisting species one of which serves as food for the other) of the "predator-prey" type under the following conditions: The food of the "prey" is unlimited, the "predator" feeds only on the "prey." The "prey" propagate in such a way that the increase in their number over a small time interval is proportional to their number. The increment in the "predators" is proportional to the product of the number of "predators" and "prey," and the natural mortality of the "predators" is proportional to their total number.

The model of such a biocoenosis is described by the following system of two nonlinear differential equations (Volterra, 1931):

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(\epsilon_1 - \gamma_{12}N_2) \\ \frac{dN_2}{dt} &= N_2(-\epsilon_2 + \gamma_{21}N_1) \end{aligned} \right\} \quad (19)$$

with $N_1(0) = (N_1)_0$; $N_2(0) = (N_2)_0$.

Here $N_1(t)$ is the number of individuals among the "prey," $N_2(t)$ is the number of individuals among the "predators," ϵ_1 is a coefficient for the natural increase in the number of "prey," ϵ_2 is a coefficient for the natural decrease in the number of

"predators" (natural mortality), γ_{12} is the competitive ability coefficient of the prey (protection coefficient), γ_{21} is the competitive ability coefficient of the "predators" (voracity coefficient). It is assumed that the coefficients in the system are positive constants which are independent of the age of the individuals, their number, and time.

The first integral of system (19) is written in the form:

$$\left(\frac{n_1}{e^{n_1}}\right)^{\epsilon_1} = C \left(\frac{n_2}{e^{n_2}}\right)^{-\epsilon_2}, \quad (20)$$

where C is a positive constant, and

$$n_1 = \frac{\gamma_{21}}{\epsilon_2} N_1; \quad n_2 = \frac{\gamma_{12}}{\epsilon_1} N_2.$$

Equation (20) is represented in the phase plane (n_1, n_2) by a closed curve (Fig. 9).

When we construct the graphs of the solution of (19) (Fig. 10) we see immediately that $N_1(t)$ and $N_2(t)$ are periodic functions of time, and that they oscillate about certain mean values: /42

$$\bar{N}_1 = \frac{\epsilon_2}{\gamma_{21}}; \quad \bar{N}_2 = \frac{\epsilon_1}{\gamma_{12}}.$$

These mean values are the solutions of system (19) with the condition

$$\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0.$$

In the case of small oscillations about the equilibrium state (\bar{N}_1, \bar{N}_2) the oscillation period is

$$T = \frac{2\pi}{\ln 2} \sqrt{t_1 t_2},$$

where t_1 is the time needed to double the number of individuals in the first species, t_2 is the time needed to reduce by one-half

the number of individuals in the second species

$$t_1 = \frac{\ln 2}{\epsilon_1}; \quad t_2 = \frac{\ln 2}{\epsilon_2}.$$

Volterra generalized the results of the mathematical study of the model system (19) in the form of the following three laws.

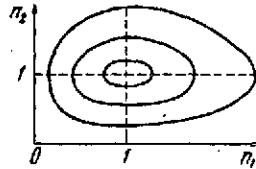


Fig. 9

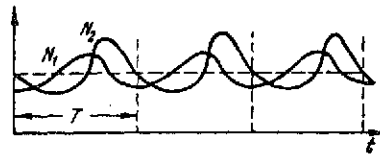


Fig. 10

Fig. 9. Phase diagram for the mutual relation of two species in a system of the "predator-prey" type (Volterra model)
Explained in text

Fig. 10. Change in the number of individuals among the "prey" and "predators" over time (t) (Volterra model)
 N_1 "prey," N_2 "predators," T oscillation period

I. The Law of Cycle Periodicity. The oscillations of two species are periodic and their period depends only on ϵ_1 , ϵ_2 , and C, i.e., on the growth and mortality coefficients, and also on the initial conditions for the number of individuals in both species.

II. The Law of the Conservation of Mean Values. The mean number of individuals in both species is constant regardless of the initial number of individuals in both species as long as the growth and mortality coefficients of both species remain constant and the conditions of attack and defense (ϵ_1 , ϵ_2 , γ_{12} , γ_{21}) remain the same.

III. The Law for the Shift in the Mean Values. If extermination (fishing, shooting) is equal and proportional to the number of individuals in both species, the mean number of the prey species will increase and the mean number of the predator species will decrease. Increased protection (fertilization, fodder, protection from pests, etc.) of the prey species increases the mean number of individuals. /43

This last law holds only in cases when $\epsilon_1 > 0$. Let $\alpha\lambda$ be the ratio of the number of individuals in the first species captured

per unit time in the biological association to the total number of individuals in this species. We will denote by $\beta\lambda$ the analogous quantity for the second species. Then the coefficients ϵ_1 , ϵ_2 in (19) will become

$$\epsilon_1 = \alpha\lambda \quad \text{and} \quad \epsilon_2 = \beta\lambda.$$

In this case we will have

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(\epsilon_1 - \alpha\lambda - \gamma_{12}N_2) \\ \frac{dN_2}{dt} &= N_2(-\epsilon_2 - \beta\lambda + \gamma_{21}N_1) \end{aligned} \right\} \quad (21)$$

When $\epsilon_1 - \alpha\lambda > 0$, there will be periodic oscillations, conversely when λ exceeds the value ϵ_1/α , i.e. when $\epsilon_1 - \alpha\lambda < 0$, there will be no oscillations and both species perish.

In the case when $\lambda = \epsilon_1/\alpha$, equations (21) give

$$\left. \begin{aligned} \frac{dN_1}{dt} &= -\gamma_{12}N_1N_2 \\ \frac{dN_2}{dt} &= N_2(-\epsilon_2^* + \gamma_{21}N_1) \end{aligned} \right\},$$

where

$$\epsilon_2^* = \epsilon_2 + \frac{\beta}{\alpha}\epsilon_1.$$

For these three cases we can construct the integral curves (Fig. 11):

- I. $N_1^{\epsilon_2} e^{-\gamma_{12}N_1} = C' N_2^{-\epsilon_1} e^{\gamma_{12}N_2}$ when $\epsilon_1 - \alpha\lambda > 0$.
- II. $N_1^{\epsilon_2} e^{-\gamma_{12}N_1} = C'' e^{\gamma_{12}N_2}$ when $\epsilon_1 - \alpha\lambda = 0$.
- III. $N_1^{\epsilon_2} e^{-\gamma_{12}N_1} = C''' N_2^{\epsilon_1} e^{\gamma_{12}N_2}$ when $\epsilon_1 - \alpha\lambda < 0$.

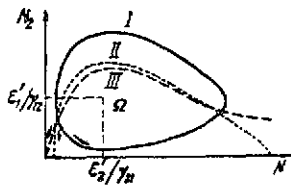


Fig. 11. Diagram for the change in the oscillation cycle for the numbers N_1 and N_2 (integral curves I, II and III)

Explained in text

We can see from Fig. 11 that when the extermination rate exceeds the limit ($\alpha\lambda = \epsilon_1$), both species perish ultimately.

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In essence model (21) which was studied by Volterra is the model for the yield collection process (continuous collection). Using this model, Volterra was able to explain quantitatively interesting phenomena which were observed in the 20's in Mediterranean fishing. Unfortunately, yield collection in which the catch coefficients are considered to be constants which increase the natural mortality coefficients of the species making up the biocoenosis (the catch coefficients do not depend on the number of individuals) cannot be used for the optimal planning of the productivity of biosystems.

2. Optimal Yield Collection in a Biosystem of the "Predator-Prey" Type

Suppose that we have a biosystem whose dynamics are described by the system of equations (19). We formulate the problem of the maximum productivity of the given biosystem. It is assumed that only the "predators" have commercial value. It is assumed that the yield is collected by catching the "predators" at some discrete instants of time so that

$$(N_2)_i^+ = (N_2)_i^- (1 - k_i),$$

where the k_i are the unknown decisions ($k_i \in [0, 1]$). We must collect the yield (catch the "predators") in such a way that the total yield collected in the time $[0, T]$ is a maximum (Yelizarov, Svirezhev, 1969).

To solve the problem we will use dynamic programming. We note that an analytical investigation of the optimal yield collection process is extremely complex for a system such as system (19). Therefore, we adopted the cybernetic model approach (investigation of the problem using "machine experiments" on an electronic digital computer).

"Machine experiments" have shown that if we study a pure Volterra system (system (19)) without constraints on the number of

"predators" and "prey," then the representative point in phase space (N_1, N_2) passes at each step when the collection is optimal from a smaller to a larger cycle, without reaching the "stationary" cycle. However, when the yield collection process is considered on a finite time interval, an optimal decision exists. However, since for any arbitrarily large time interval the system does not reach the stationary state as the yield is collected and passes to cycles with a constantly increasing number of "prey," the practical value of such a model is very doubtful (in real biological systems, the number of "prey" is always bounded above, due to the limited area, epizooty, etc.).

3. Optimal Yield Collection in a Biosystem of the "Predator-Prey" Type (Other Models) /45

Let us try to augment the Volterra model by introducing certain constraints in order to have a stationary state for collecting the yield. We will consider several types of constraints:

Constraints on the Rate at which the "Prey" Propagate

We will analyze the following system:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= v - \gamma_{12} N_1 N_2 \\ \frac{dN_2}{dt} &= N_2 (-\epsilon_1 + \gamma_{21} N_1) \\ v &= \begin{cases} \epsilon_1 N_1, & \text{when } N_1 < \frac{v_0}{\epsilon_1} \\ v_0, & \text{when } N_1 \geq \frac{v_0}{\epsilon_1} \end{cases} \end{aligned} \right\}. \quad (22)$$

The coefficients ϵ_1 , ϵ_2 , γ_{12} , γ_{21} have the same meaning as in system (19), but in contrast to system (19) when the number of "prey" exceeds a certain limit, the rate at which they propagate becomes constant and does not depend on the number of the "prey". The phase trajectories of this system for various initial conditions are plotted in Fig. 12. It is easily seen that depending on the initial conditions two states are possible: If $(N_1)_0 < v_0/\epsilon_1$, system (22) is fully analogous to system (19) described above, if $(N_1)_0 \geq v_0/\epsilon_1$, system (22) has a quasilimiting cycle (the trajectory touches this cycle) for which $N_1 = v_0/\epsilon_1$, and its equation is equation (20) of the Volterra cycle with the appropriate coefficients.

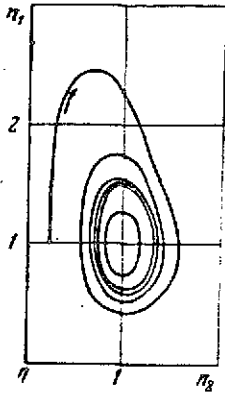


Fig. 12. Family of phase trajectories of the system describing the change in the number of "predators" and "prey" when the propagation rate of the "prey" is constrained

$$\begin{aligned} n_1 &= \frac{\gamma_{21}}{\epsilon_2} N_1; \\ n_2 &= \frac{\gamma_{12}}{\epsilon_1} N_2; \quad \epsilon_2 = 2 \quad 1/h, \\ \epsilon_1 &= 1 \quad 1/h, \quad \gamma_{12} = 0.05 \quad 1/h \\ \gamma_{21} &= 0.001 \quad 1/h, \quad v_0 = 3 \quad 000 \end{aligned}$$

When we formulate the optimal yield collection problem for system (22), numerical calculations show that in this system just as in the system considered above, the representative point in the collection process passes at each step to ever larger cycles.

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Thus, the constraint on the propagation rate of the "prey" of the type given above does not allow us to obtain in a certain sense a "stationary" state for the yield collection process of the "predators." Therefore for the reasons which were given for system (19), system (22) cannot be used as the model in the study of the optimal yield collection of "prey" in a biosystem of the "predator-prey" type.

Bounds on the Number of "Prey"

We will consider the optimal yield collection process for the case when the dynamics of the system are described by equations (19) with the additional condition that $N_1 \leq N_1^*$, i.e., the number of "prey" is bounded above (where, for example, N_1^* denotes that level of the number of "prey" above which various types of epidemic or other unfavorable phenomena for this species occur in the population).

It is easily shown that this system when it reaches the limit $N_1 = N_1^*$ behaves as a population (in this case the population of "predators") whose size increases or decreases exponentially (depending on the values of the coefficients ϵ_2 , γ_{21} and the value N_1^*).

System (19) with the bound $N_1 \leq N_1^*$ also has no "stationary" state for collecting the yield. Thus, if $\gamma_{21} N_1^* > \epsilon_2$, for finite T (T is the time during which the yield is collected in the system)

the optimal decision after the system reaches the bound is as follows: $k \equiv 0$ almost everywhere, except at $t = T$, where $k = 1$. When $\gamma_{21} N_1^* < \epsilon_2$, $k = 1$ at the instant t^* when the system reaches the bound, and subsequently $k \equiv 0$. When $\gamma_{21} N_1^* = \epsilon_2$, $k = 0$ almost everywhere except at a single point $t \in [t^*, T]$, where $k = 1$.

Thus, even in the case when there is a bound on the number of "prey" it is not possible to obtain in system (19) a "stationary" yield collection process which has practical value.

Introduction of a New Criterion Function

We will introduce into the discussion a new criterion function which will take into account that the yield collected are both individuals among the "predators" and among the "prey." When c_1 and c_2 are some cost coefficients ($c_1, c_2 > 0$) per unit biomass of the "prey" and "predators" respectively, the yield per step is expressed in the form

$$g_i = (k^1)_i c_1 (N_1)_i^- + (k^2)_i c_2 (N_2)_i^-, \quad (23)$$

where $(k^1)_i, (k^2)_i \in [0, 1]$ are the admissible decisions in the step and $(N_1)_i^-$ and $(N_2)_i^-$ are the values of the state variables in the i -th step to the left of the instant t_i when the yield is collected. /47
The total yield, whose maximum value must be determined, is equal to

$$G = \sum_{i=1}^n q_i.$$

Computations have shown that the optimal yield collection process for the Volterra model with the criterion function (23) is as follows: the larger the cycle which is considered, the larger can be the yield collected (the collection is carried to the lowest level into which the state space can be broken up both for the "predators" and the "prey"). The representative point in the collection process makes a transition to ever increasing cycles. This version is also uninteresting, since it does not yield a "stationary" yield collection process.

Bound on the Number of "Predators" and "Prey"
Due to Interspecific Competition
(Kostitzin Model)

When interspecific competition among the "predators" and "prey" is taken into account, we are lead to a consideration of the the system (Kostitzin, 1937):

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(\varepsilon_1 - \gamma_{12}N_2 - \gamma_{11}N_1) \\ \frac{dN_2}{dt} &= N_2(-\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2) \end{aligned} \right\} \quad (24)$$

Here γ_{11} , γ_{22} are coefficients which take into account inter-specific competition. All coefficients of system (24) are positive. When the conditions a) and b) below are satisfied

a) $\varepsilon_1\gamma_{21} > \varepsilon_2\gamma_{11},$

b) $[\varepsilon_1\gamma_{22}(\gamma_{11} - \gamma_{21}) + \varepsilon_2\gamma_{11}(\gamma_{12} + \gamma_{22})]^2 \geq 4\gamma_{12}\gamma_{21}(\varepsilon_1\gamma_{22} + \varepsilon_2\gamma_{12}) \times$
 $\times (\varepsilon_1\gamma_{21} - \varepsilon_2\gamma_{11})$

system (24) has a stable limiting point (node) and the coordinates of the point are positive and different from zero. This means that the system is damped to such an extent that there are no oscillations in the number of species, and that their number varies monotonically over time. When the optimal yield collection (discrete collection) problem is formulated for system (24), then for the case when only the "predators" have commercial value, i.e., when the criterion function per step has the form

$$g_i = (k^2)_i \cdot (N_2)_i,$$

the optimal yield collection process consists of the following: the collection goes on up to the lowest level into which the state space for the number of "predators" can be broken up, and the lower this level, the greater the yield collected. "Stationary" collection does not take place.

From the standpoint of the practical value of the result obtained, the most interesting yield collection process is the process for the model described by system (24) with a criterion function of the form (23), where $c_1, c_2 > 0$, i.e. when both the "predators"

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and the "prey" have productive value.

In this case after a very short transition process (one or two steps) the yield collection becomes "stationary" and the collection for each species is analogous to the yield collection in homogeneous populations which are described by logistic curves.

The dependence of the total yield on the step size for the process is given in Fig. 13. This diagram shows that the maximum yield, just as in the cases considered in Chapter II, is obtained when the collection is continuous.

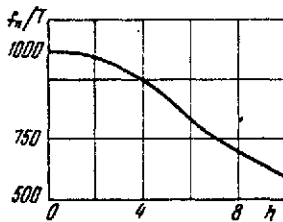


Fig. 13. The total yield (f_n) in the "predator-prey" system versus the step size $h(N_1)_0 = 1000$, $(N_2)_0 = 10$, $\epsilon_1 = 2$ l/h, $\epsilon_2 = 1$ l/h, $\gamma_{11} = \gamma_{12} = \gamma_{21} = 0.001$ l/h, $\gamma_{22} = 0.01$ l/h, $C_1 = 1$, $C_2 = 50$, $T = 500$ h) (reduced to unit time T)

4. Numerical Solution of the Optimal Yield Collection Problem in a Biosystem of the "Predator-Prey" Type

The optimal yield collection problem in a biocoenosis of the "predator-prey" type will be solved numerically for model (24) in accordance with the following algorithm:

1. We construct a scale of states $\{N^{i,j}(0)\} = \{N_1^i \times N_2^j\}$, where $i = 1, 2, \dots, m$, $j = 1, 2, \dots, p$.
2. We introduce into the discussion the quantities $G_t^{i,j}$ ($G_t^{i,j}$ the maximum yield of "predators" and "prey" in t steps for the (i,j) -th node of the scale of states. At the initial instant of time we set $G_0^{i_{data}, j_{data}} = 0$ and $G_0^{i,j} = -1$ for all nodes $i \neq i_{data}$ and $j \neq j_{data}$.
3. We construct a transition matrix for the change of state of the variables from one level to another over time $N_{12}^{i_1, j_1}$ ($i_1 = 1, 2, \dots, m$; $j_1 = 1, 2, \dots, p$) by integrating numerically system (24) over one yield collection step.
4. For all nodes ($i_1 = 1, 2, \dots, m$, $j_1 = 1, 2, \dots, p$) of the scale of states which can be reached from the (i,j) -th node ($G_{t-1}^{i,j} \geq 0$), we compute the value of the criterion function, and using Bellman's optimality principle we find the maximum total yield

over all nodes of the $t - 1$ -th level over time in t collection steps.

5. We calculate the optimal decisions in the form of the matrix $MK_{1,2}^{i,j}$ in the t -th level over time.

6. Printing out at each step over time the return matrices (G_{\max}) and the optimal decision matrix (MK), we analyze the computational results and determine the optimal paths for the state variables, the optimal policy and the total maximum yield collected in $t = 1, 2, \dots, n$ steps.

This algorithm was programmed for an electronic digital computer (Program 4) in the ALGOL-60 language.

Program 4

```

begin integer i, j, i1, j1, i2, j2, l, m, n, p, t, idata, jdata;
  real N1up, N1down, N2up, N2down, D, Dmax, T, eps1, eps2,
  gamma 11, gamma 12, gamma 21, gamma 22;
  array MK, N12 [1 : m, 1 : p, 1 : 2], G, Gmax [1 : m, 1 : p],
  C [1 : 2], N1 [1 : m], N2 [1 : p], N, Nfin [1 : 2];
  procedure runge (x, y, r, f, eps, eta, prim, xfin) result (yfin);
    Comment: The Runge-Kutta procedure is described in
  procedure f (x, y, r, z);
    value x, y, r; real x; integer r; array y, z;
    begin z [1] := (eps1 - gamma 12 × y [2] - gamma 11 × y [1]) × y [1];
      z [2] := (gamma 21 × y [1] - eps2 - gamma 22 × y [2]) × y [2]
    end;
    for i := 1 step 1 until m do
      N1 [i] := (N1up - N1down) × (i - 1) / (m - 1);
    for j := 1 step 1 until p do
      N2 [j] := (N2up - N2down) × (j - 1) / (p - 1);
    Comment The scale of states has been constructed
    for i := 1 step 1 until m do
      for j := 1 step 1 until p do
        begin N [1] := N1 [i]; N [2] := N2 [j];
          runge (0, N, 2, f, eps, eta, true, T/n, Nfin);
          for l := 1, 2 do N12 [i, j, l] := Nfin [l];
          G [i, j] := -1.0
        end; G [idata, jdata] := 0;
    Comment: The transition matrix for the change of state of
      the state variables over time from one level to
      another has been constructed & the
    begin for t := 1 step 1 until n do
      for i := 1 step 1 until m do
        for j := 1 step 1 until p do
          initial return matrix has been set
          up
          begin Dmax := 0;
            for i1 := 1 step 1 until m do
              for j1 := 1 step 1 until p do
                begin D := (if G [i1, j1] < 0 ∨
                  N12 [i1, j1, 1] < N1 [i1] ∨
                  N12 [i1, j1, 2] < N2 [j1] then -1.0 else
                  C [1] × (N12 [i1, j1, 1] - N1 [i1]) +
                  C [2] × (N12 [i1, j1, 2] - N2 [j1]) +
                  G [i1, j1]);
                  if D < Dmax then go to L1;
                  Dmax := D; i2 := i1; j2 := j1
                end
              end
            end
          end
        end
      end
    end
  end

```



```

L1:      end; Gmax [i, j]:=Dmax;
        MK [i, j, 1]:=(N12 [i2, j2, 1] - N1 [i])/N12 [i2, j2, 1]; MK
          [i, j, 2]:=
        (N12 [i2, j2, 2] - N2 [i])/ (N12 [i2, j2, 2]);
        if MK [i, j, 1] < 0  $\vee$  MK [i, j, 2] < 0 then
          MK [i, j, 1]:=MK [i, j, 2]:=-1.0
        end;
        print (t, MK, Gmax);
        for i:=1 step 1 until m do
          for j:=1 step 1 until p do
            G [i, j]:= Gmax [i, j]
          end j
        end i
      end t
    end program,

```

The computational results which were obtained using the above program for various h are plotted in Fig. 13.

Thus, the following conclusion can be made: when the optimal yield collection process is studied in a biosystem of the "predator-prey" type, we must use mathematical models of the type (24) (models of this type which also include models for more general cases were proposed for the first time by V. A. Kostitzin (Kostitzin, 1937) with criterion functions of the type (23).

We will state one proposition which is not proved rigorously but which is probable according to the results obtained from "machine experiments."

Often natural biocoenoses or biogeocoenoses are in stable dynamic equilibrium at the instant when external intervention takes place (for example, the yield is collected in a particular species). When the stationary state exists for the yield collection process, the transition to this state from the initial state takes place, as many calculations on an electronic digital computer have shown, in one step without collecting the yield, i.e., in a time which is much shorter than the time in which the biocoenosis production is used (the yield is collected). Consequently in those cases when the sizes of the species which make up the biocoenosis vary over time aperiodically without oscillations, and a stationary yield collection process exists, Bellman's optimality principle can be replaced by the simpler "local optimality" principle (optimality in one step) without committing a large error, and the very complex dynamic programming procedure is replaced by the local optimization procedure.

In this chapter we considered optimization problems for two-component biosystems. Historically it so happened that the models of such biosystems have always been studied as models of the simplest biocoenoses consisting of two species, one of which serves as food for the other ("predator-prey"). But, as we already have shown above, such models are essentially models of biogeocoenoses (or some subsystems of these), i.e., biosystems consisting of an

association of live organisms and their environment. Therefore, depending on the context, we will call the same mathematical models in one case biocoenosis models and in the other biogeocoenosis models, preferring, of course, the more general term biosystem.

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CHAP. IV. STATIONARY YIELD COLLECTION PROCESSES

In the preceding chapter we already dwelt on the problem of the importance of stationary states in the utilization of biosystems. In fact, the stationary yield collection process ensures both the preservation of the biogeocoenosis over a sufficiently long time period, and from the economic point of view the very important rhythm and qualitative constancy of the utilization process itself. Therefore, we considered it useful to investigate stationary yield collection processes in a separate chapter.

1. Yield Collection in a Biosystem of the "Predator-Prey" Type. Stationary Process with a Small Fixed Step.

Suppose we have a biosystem of the "predator-prey" type, the dynamics of which are described by the system of differential equations (24) (Chap. III). When certain conditions are satisfied, these equations describe the aperiodic change in the number of "predators" and "prey" in the biocoenosis.

We will formulate the problem of maximizing the productivity of the given biocoenosis (the problem of maximizing some criterion function) over a sufficiently large but finite time interval $[0, T]$. It is assumed that the yield collected (both "predators" and "prey" are collected) is a discrete process with a sufficiently small step $h = \Delta t = T/n$ (n is large) and that the yield collection procedure "does not deteriorate" the biocoenosis, i.e., the number of individuals in each species is and remains a non-decreasing function of time. By a decision in the given system we shall mean the yield collected, i.e., the collection of a certain amount of "predator" and "prey" biomasses with their subsequent removal from the reproductive cycle (Yelizarov, Svirezhev, 1968; Jelisarov, 1969).

Many "machine experiments" have shown that in such a system an optimal yield collection process exists which becomes quickly stationary, so that for T sufficiently large and Δt sufficiently small, the process can be considered to be stationary from the very beginning with a great degree of accuracy. The requirement that the criterion function be maximized (the total yield collected over the time T) is replaced by the "local optimality" requirement (the requirement that the criterion function be a maximum in one step). In fact, for sufficiently small Δt we can write:

$$\left. \begin{aligned} \Delta N_1 &\simeq N_1(\varepsilon_1 - \gamma_{12}N_2 - \gamma_{11}N_1)\Delta t \\ \Delta N_2 &\simeq N_2(-\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2)\Delta t \end{aligned} \right\}.$$

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The criterion function (the total yield) can be written in the form

$$G = \sum_{i=1}^n \sum_{j=1}^r c_j (\Delta N_j)_i,$$

where n is the number of collection steps, r is the number of species in the biocoenosis, $c_j \geq 0$ is the unit cost for the biomass of the j -th species, ΔN_j is the increment in the biomass of the j -th species in one step.

We introduce the new criterion function $I = G/T$, which defines the return in one step (as a unit of time) for the stationary yield collection process. This replacement simplifies intermediate calculations without changing the final results. Thus,

$$I \simeq c_1 N_1 (\varepsilon_1 - \gamma_{12} N_2 - \gamma_{11} N_1) + c_2 N_2 (-\varepsilon_2 + \gamma_{21} N_1 - \gamma_{22} N_2). \quad (25)$$

On the basis of the assumption that the derivatives of the species sizes with respect to time are nonnegative, and from the fact that only positive values of these numbers make sense (the condition that the biocoenosis "does not deteriorate"), it follows that the maximum I (if it exists) must be attained in the region Ω determined by the inequalities:

$$\left. \begin{aligned} \varepsilon_1 - \gamma_{12} N_2 - \gamma_{11} N_1 &\geq 0 \\ -\varepsilon_2 + \gamma_{21} N_1 - \gamma_{22} N_2 &\geq 0 \\ N_1 &> 0, \quad N_2 &\geq 0 \end{aligned} \right\}. \quad (26)$$

We will call this region the "feasible" region.

We can easily see that the criterion function (25) is nonlinear and the constraints (26) are linear, so that the problem of finding the maximum I is a typical nonlinear programming problem (Kunzi, Krelle, 1965; Carr, Howe, 1966). In the case when the stability condition

$$\varepsilon_1 \gamma_{21} > \varepsilon_2 \gamma_{11},$$

is satisfied, the feasible region Ω determined by the inequalities (26) is the region ΔKLM (Fig. 14).

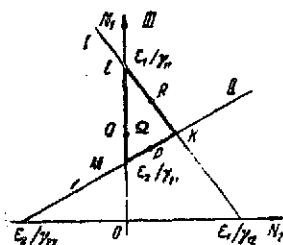


Fig. 14. Feasible region $\Omega(\Delta KLM)$

Explanation in text.

To simplify the discussion we assume that $\gamma_{12} = \gamma_{21}$. Taking partial derivatives of I with respect to N_1 and N_2 and equating these to zero to obtain the necessary condition for the existence of the extremum, we find in the plane (N_1, N_2) the point (N_1^0, N_2^0) which is a candidate for the extremum.

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$$\left. \begin{aligned} N_1^0 &= \frac{2c_1c_2\gamma_{11}\gamma_{22} - \gamma_{21}^2(c_2 - c_1)}{4c_1c_2\gamma_{11}\gamma_{22} - \gamma_{21}^2(c_2 - c_1)^2} \\ N_2^0 &= \frac{2c_1c_2\gamma_{11}\gamma_{22} - \gamma_{21}^2(c_2 - c_1)}{4c_1c_2\gamma_{11}\gamma_{22} - \gamma_{21}^2(c_2 - c_1)^2} \end{aligned} \right\} \quad (27)$$

A necessary and sufficient condition that the maximum occur at the point (N_1^0, N_2^0) (the concavity of the criterion function in the neighborhood of the point (N_1^0, N_2^0)) is that the following condition be satisfied for the second partial derivatives:

$$I_{N_1N_1}'' < 0; \quad \begin{vmatrix} I_{N_1N_1}'' & I_{N_1N_2}'' \\ I_{N_2N_1}'' & I_{N_2N_2}'' \end{vmatrix} > 0.$$

It is easily seen that the first inequality is satisfied, and the second inequality implies that it holds when

$$\frac{c_1}{c_2} + \frac{c_2}{c_1} - 2 < \frac{4\gamma_{11}\gamma_{22}}{\gamma_{21}^2}.$$

We introduce the notation:

$$\alpha = \frac{c_1\gamma_{11}}{c_2\gamma_{21}}; \quad \beta = \frac{c_2\gamma_{22}}{c_1\gamma_{21}}.$$

Then

$$\frac{c_1}{c_3} + \frac{c_3}{c_1} - 2 < 4\alpha\beta. \quad (28)$$

This means that a necessary and sufficient condition that the criterion function I attain its maximum in the plane (N_1, N_2) is that the two costs c_1 and c_2 satisfy inequality (28).

We will try to determine under which conditions the critical point (N_1^0, N_2^0) of the criterion function I lies in the feasible region Ω determined by the inequalities (26). We substitute the coordinates of the critical points (27) in (26) and take into account that $\gamma_{12} = \gamma_{21}$: /54

$$\left. \begin{aligned} \varepsilon_1 - \frac{\gamma_{21} [\varepsilon_1 \gamma_{21} c_1 (c_2 - c_1) - 2c_1 c_2 \varepsilon_2 \gamma_{11}]}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} - \\ - \frac{\gamma_{11} [2c_1 c_2 \varepsilon_1 \gamma_{22} - \varepsilon_2 \gamma_{21} c_2 (c_2 - c_1)]}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} > 0 \\ - \varepsilon_2 + \frac{\gamma_{21} [2c_1 c_2 \varepsilon_1 \gamma_{22} - \varepsilon_2 \gamma_{21} c_2 (c_2 - c_1)]}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} - \\ - \frac{\gamma_{22} [\varepsilon_1 \gamma_{21} c_1 (c_2 - c_1) - 2c_1 c_2 \varepsilon_2 \gamma_{11}]}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} > 0 \\ \frac{2c_1 c_2 \varepsilon_1 \gamma_{22} - \varepsilon_2 \gamma_{21} c_2 (c_2 - c_1)}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} > 0 \\ \frac{\varepsilon_1 \gamma_{21} c_1 (c_2 - c_1) - 2c_1 c_2 \varepsilon_2 \gamma_{11}}{4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2} > 0 \end{aligned} \right\}.$$

We assume for definiteness that the denominator which is the same in all these inequalities is positive, i.e.,

$$\begin{aligned} 4c_1 c_2 \gamma_{11} \gamma_{22} - \gamma_{21}^2 (c_2 - c_1)^2 > 0, \\ \frac{4\gamma_{11} \gamma_{22}}{\gamma_{21}^2} > \frac{(c_2 - c_1)^2}{c_1 c_2}, \\ 4\alpha\beta > \frac{c_3}{c_1} + \frac{c_1}{c_3} - 2. \end{aligned}$$

But this is the inequality (28) which was obtained above. Now the study of the four inequalities given above becomes simpler. Multiplying them by the denominator and equating like terms we obtain the system

$$\left. \begin{aligned} 2c_1c_2e_1\gamma_{11}\gamma_{22} - c_1^2e_1\gamma_{21}^2 + c_1c_2e_1\gamma_{21}^2 + c_1c_2e_2\gamma_{11}\gamma_{21} + c_2^2e_2\gamma_{11}\gamma_{21} &> 0 \\ -2c_1c_2e_2\gamma_{11}\gamma_{22} + c_1^2e_2\gamma_{21}^2 - c_1c_2e_2\gamma_{21}^2 + c_1c_2e_1\gamma_{22}\gamma_{21} + c_1^2e_1\gamma_{22}\gamma_{21} &> 0 \\ 2c_1c_2e_1\gamma_{23} - e_2\gamma_{21}c_2(c_2 - c_1) &> 0 \\ e_1\gamma_{21}c_1(c_2 - c_1) - 2c_1c_2e_2\gamma_{11} &> 0 \end{aligned} \right\}.$$

Dividing the first inequality by c_2^2 , the second by c_1^2 , the third and fourth by $c_1 \cdot c_2$ we reduce the system of inequalities to the form:

$$\left. \begin{aligned} \frac{c_1}{c_2} &> \frac{e_1\gamma_{21}^2 - e_2\gamma_{11}\gamma_{21}}{2e_1\gamma_{11}\gamma_{22} + e_1\gamma_{21}^2 + e_2\gamma_{11}\gamma_{21}} \\ \frac{c_1}{c_2} &> \frac{e_2\gamma_{21}^2 + 2e_2\gamma_{11}\gamma_{22} - e_1\gamma_{22}\gamma_{21}}{e_1\gamma_{22}\gamma_{21} + e_2\gamma_{21}^2} \\ \frac{c_1}{c_2} &> \frac{1}{1 + 2 \frac{e_1\gamma_{22}}{e_2\gamma_{21}}} \\ \frac{c_1}{c_2} &< 1 - 2 \frac{e_2\gamma_{11}}{e_1\gamma_{21}} \end{aligned} \right\}$$

or equivalently to

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$$\left. \begin{aligned} \frac{c_1}{c_2} &> \frac{1-x}{(1+2\beta)x} \\ \frac{c_1}{c_2} &> \frac{1-(1-2x)\beta}{1+\beta} \\ \frac{c_1}{c_2} &> \frac{1}{2-2\beta} \\ \frac{c_1}{c_2} &< 1-2\alpha \end{aligned} \right\}.$$

It can be shown that if the last of these inequalities is satisfied, the first three inequalities are valid for any $\beta > 0$ and $c_1/c_2 > 0$.

Thus, a necessary and sufficient condition that the critical point (N_1^0, N_2^0) of the criterion function lie in the region Ω and that at this point the criterion function attain its maximum value is that the following system of inequalities be satisfied:

$$\left. \begin{aligned} \frac{c_1}{c_2} &> 0; & \frac{c_1}{c_2} &< 1 - 2\alpha \\ \frac{c_1}{c_2} + \frac{c_2}{c_1} - 2 &< 4\alpha^3 \end{aligned} \right\} \quad (29)$$

It is interesting to determine the limiting relations among the internal parameters of system (24) for which the extremum point (N_1^0, N_2^0) belongs to the region Ω . Writing the second and third inequalities from (29) in the form of equalities, and eliminating c_1/c_2 , we obtain

$$\alpha = \frac{3}{1+2\beta} \quad (30)$$

This equality determines the maximum permissible relations between the parameters of system (24) for which for given values c_1/c_2 , the extremum point of the criterion function will lie in the region Ω .

Figure 15 shows the curve $\alpha = f(1/\beta)$ which can be used to determine with the given coefficients from system (24) the admissible boundaries for the change in the cost ratio c_1/c_2 for which the point (N_1^0, N_2^0) lies in the interior of the region Ω . /56

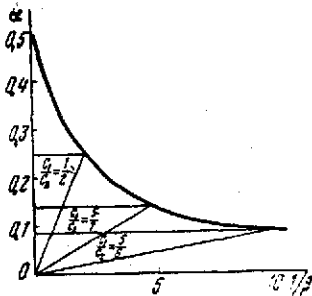


Fig. 15. Nomogram for determining the admissible boundaries for the change in the cost ratio c_1/c_2 from the given coefficients of system (24)

Explained in text

When $\alpha > \beta/(1 + 2\beta)$, the extremum point (N_1^0, N_2^0) does not lie in the interior of the region Ω for any cost ratio c_1/c_2 . In this case the criterion function I attains its maximum on the boundary of the region Ω which is determined by the straight lines

- (I) $\gamma_{11}N_1 + \gamma_{12}N_2 = \varepsilon_1$,
- (II) $\gamma_{21}N_1 - \gamma_{22}N_2 = \varepsilon_2$,
- (III) $N_2 = 0$.

The coordinates of the vertices of the triangle KLM are easily determined:

$$\begin{aligned} N_{1K} &= \frac{\varepsilon_1 \gamma_{22} + \varepsilon_2 \gamma_{21}}{\gamma_{21}^2 + \gamma_{11} \gamma_{22}}; & N_{2K} &= \frac{\varepsilon_1 \gamma_{21} - \varepsilon_2 \gamma_{11}}{\gamma_{21}^2 + \gamma_{11} \gamma_{22}}; \\ N_{1L} &= \frac{\varepsilon_1}{\gamma_{11}}; & N_{2L} &= 0 \\ N_{1M} &= \frac{\varepsilon_2}{\gamma_{21}}; & N_{2M} &= 0. \end{aligned}$$

The values of the criterion function (25) at the extreme points of the region Ω are equal to

$$\begin{aligned} I_K &= I_L = 0, \\ I_M &= \frac{\varepsilon_2 (\gamma_{21} \varepsilon_1 - \varepsilon_2 \gamma_{11})}{\gamma_{21}^2} \cdot c_1. \end{aligned}$$

We will investigate the behavior of the function I on the lines I, II, III. We will show that on the line I the function I has a unique stationary point (the point for the maximum). To prove it we will proceed as follows: we express one variable in terms of another variable (for example, N_1 in terms of N_2), and using coupling equation (I), substitute this value of N_1 in equation (25). By eliminating one variable we reduced the function I of two variables to a function of a single variable.

It is known that the criterion function I takes on equal values at the points K and L ($I_K = I_L = 0$). By Rolle's theorem there will be a point R between the points K and L on the line I, $R(L < R < K)$, such that $I'(R) = 0$. The point R is easily determined. Its coordinates are

$$\left. \begin{aligned} N_{1R} &= \frac{2\varepsilon_1 \gamma_{11} \gamma_{22} + \varepsilon_1 \gamma_{21}^2 + \varepsilon_2 \gamma_{21} \gamma_{11}}{2\gamma_{11} (\gamma_{21}^2 + \gamma_{11} \gamma_{22})} \\ N_{2R} &= \frac{\varepsilon_1 \gamma_{21} - \varepsilon_2 \gamma_{11}}{2(\gamma_{21}^2 + \gamma_{11} \gamma_{22})} \end{aligned} \right\}.$$

The value of the criterion function at this point is equal to

$$I_R = \frac{(\varepsilon_1 \gamma_{21} - \varepsilon_2 \gamma_{11})^2}{4\gamma_{11} (\gamma_{21}^2 + \gamma_{11} \gamma_{22})} \cdot c_2.$$

Using the elimination method, it can be shown that the function I has also a unique stationary point (maximum point) P with the coordinates

$$\left. \begin{aligned} N_{1P} &= \frac{e_1 \gamma_{22} + e_2 \gamma_{21}}{2(\gamma_{21}^2 + \gamma_{11} \gamma_{21})} \\ N_{2P} &= \frac{e_1 \gamma_{22} \gamma_{21} - e_2 \gamma_{21}^2 - 2e_2 \gamma_{11} \gamma_{22}}{2(\gamma_{21}^2 + \gamma_{11} \gamma_{22}) \gamma_{22}} \end{aligned} \right\}.$$

on the straight line II.

The point P can lie either on the segment KM or not on it (to the left of the point M).

If $N_{2P} < 0$, the value of the criterion function at the point P is equal to

$$I_P = \frac{(e_1 \gamma_{22} + e_2 \gamma_{21})^2}{4\gamma_{22}(\gamma_{21}^2 + \gamma_{11} \gamma_{22})} \cdot c_1.$$

But if $N_{2P} \leq 0$, the maximum value of I on the straight line II is attained at the point M.

On the straight line III the function I has also a unique critical point (for the maximum) Q with the coordinates

$$N_{1Q} = \frac{e_1}{2\gamma_{11}}; \quad N_{2Q} = 0.$$

Since the point M lies on the straight line III, it can be easily shown that,

$$I_Q \geq I_M, \quad \text{where} \quad I_Q = \frac{e_1^2}{4\gamma_{11}} c_1.$$

Since the maximum I on the lines II and III depends only on one cost c_1 , it is natural to compare first I_P and I_Q . We will show that $I_Q > I_P$. The proof will be by contradiction.

Let $Q \in \Omega$, $P \in \Omega$ and

$$I_Q \leq I_P.$$

Subtracting I_P from I_Q , we have

$$\varepsilon_1^2 \gamma_{21} \gamma_{32} - 2\varepsilon_1 \varepsilon_2 \gamma_{11} \gamma_{32} - \varepsilon_2^2 \gamma_{11} \gamma_{21} \leq 0$$

and

$$0 < \varepsilon_1 \leq \varepsilon_2 \frac{\gamma_{11} \gamma_{32} + \sqrt{\gamma_{11}^2 \gamma_{32}^2 + \gamma_{11} \gamma_{32} \gamma_{21}^2}}{\gamma_{21} \gamma_{32}}.$$

The last inequality implies $N_{2P} < 0$, i.e., $P \notin \Omega$, which contradicts the given condition. Thus, on the lines II and III the maximum I is always attained only at the point Q .

To find the absolute maximum of the function I on the boundary of the region Ω we must only compare I_R and I_Q . Then

$$I^* = \max\{I_Q, I_R\} = \frac{\varepsilon_1^3}{4\gamma_{11}} \cdot \max\{c_1, \Gamma c_2\},$$

where

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$$\Gamma = \frac{(\gamma_{21}\varepsilon_1 - \gamma_{11}\varepsilon_2)^2}{\varepsilon_1^3(\gamma_{21}^2 + \gamma_{11}\gamma_{32})}.$$

From here, if $c_1 < \Gamma c_2$, I attains the maximum at the point Q . If $c_1 > \Gamma c_2$, I attains the maximum at the point R .

Thus, depending on the coefficients of system (24) whose values are determined by the internal structure of the biocoenosis, the criterion function (25) considered by us can attain its maximum either in the interior of the region Ω , or on its boundary.

In the first case the maximum I is attained at the point (N_1^0, N_2^0) and the optimum yield collection process consists of removing the increment in the "predator" and the "prey" biomass from the system in one step of the process up to the levels determined by the corresponding coordinates of the critical point (N_1^0, N_2^0) .

In the second case, depending on the ratio of the costs per unit biomass collected which is determined by external factors,

and also depending on the relations among the coefficients in system (24) which are determined by the internal structure of the biocoenosis, two types of optimal decisions can be made, namely:

a) if the maximum of I is attained at the point R , the process in which both the number of "predators" and "prey" are maintained at some constant levels determined by the coordinates of the point R is optimal, and the yield which is collected is only the increment in the "predator" biomass per unit time which is determined by the step in the process, since the biomass increment in the "prey" at this point is equal to zero.

b) If I attains the maximum at the point Q , the stationary optimal yield collection process consists of creating a situation in which there are no "predators" and the number of "prey" is maintained on a constant level equal to $\epsilon_1/2\gamma_{1P}$ when the increment in the "prey" biomass is collected in one step of the process.

2. Lower Bound on the Number of "Predators" ("Health" Norm)

It should be noted that when real biosystems are described a somewhat different region is characteristic in defining the system of equations (24), and consequently also in defining the criterion function (25). It must include a constraint on the minimum number of "predators" needed to prevent epizooty among the "prey." Therefore, instead of the constraints (26) we must consider constraints of the following form:

$$\left. \begin{aligned} \epsilon_1 - \gamma_{12}N_2 - \gamma_{11}N_1 &\geq 0 \\ -\epsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2 &\geq 0 \\ N_1 &> 0; \quad N_2 > a > 0 \end{aligned} \right\}, \quad (31)$$

where a is some "health" norm for the number of "predators" for the given biocoenosis.

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When we study the problem of maximizing the criterion function (25) in the region bounded by (31), we see easily (Fig. 16) that if the maximum of I is attained in the interior of the region $\Omega'(\triangle ABK)$ then the sufficient condition for the existence of the extremum coincides with (28)

Taking into consideration the constraints $N_2 \geq a > 0$, we will clarify the conditions when the critical point (N_1^0, N_2^0) lies in the region Ω' . Proceeding analogously as above, it can be shown that in order that the stationary point (N_1^0, N_2^0) lie in the interior

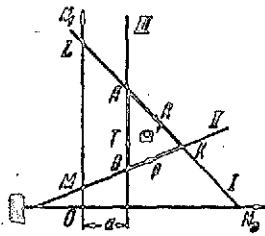


Fig. 16. Feasible region Ω' ($\triangle ABK$) determined by (31)

of the region Ω' and that the criterion function I take on a maximum value at this point, a necessary and sufficient condition is that the parameters of system (24) and the cost ratio c_1/c_2 satisfy the following system of inequalities:

$$\left. \begin{aligned} \frac{c_1}{c_2} + \frac{c_2}{c_1} - 2 &< 4\alpha\beta \\ S &< \frac{1 - \frac{c_1}{c_2} - 2\alpha}{2 + 4\alpha\beta - \frac{c_1}{c_2} - \frac{c_2}{c_1}} \end{aligned} \right\} \quad (32)$$

where

$$S = \frac{\gamma_{21} a}{s_1}$$

If the inequalities (32) are not satisfied, I attains the maximum on the boundary of the region Ω' . A study of the behavior of the criterion function on the boundary of the region Ω' has shown that depending on the internal properties of system (24), and on the external action on it by means of controlling the cost ratio c_1/c_2 per unit biomass removed for both species, the following cases can occur (see Fig. 16):

1. If $N_{1T} > N_{1B}$, the maximum value of the criterion function is equal to:

$$\begin{aligned} \text{a) } N_{2R}, N_{2P} > a, \text{ then} \\ I^* &= \max \{I_T, J_P, I_R\}, \end{aligned}$$

where I_T, I_P, I_R are maximum values of the function I on the corresponding lines:

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b) If $N_{2R}, N_{2P} \leq a$, then

$$I^* = \max \{I_A, I_B, I_T\}.$$

c) If $N_{2R} \leq a, N_{2P} > a$, then

$$I^* = \max \{I_A, I_T, I_P\} = \max \{I_T, I_P\}.$$

d) If $N_{2R} > a, N_{2P} \leq a$, then

$$I^* = \max \{I_R, I_T, I_B\} = \max \{I_R, I_T\}.$$

2. If $N_{1T} \leq N_{1B}$, the maximum value of the function I is equal to

a) If $N_{2R}, N_{2P} > a$, then

$$I^* = \max \{I_B, I_P, I_R\} = \max \{I_P, I_R\}.$$

b) If $N_{2R}, N_{2P} \leq a$, then

$$I^* = \max \{I_A, I_B, I_T\} = \max \{I_A, I_B\}.$$

c) If $N_{2R} \leq a, N_{2P} > a$, then

$$I^* = \max \{I_A, I_B, I_P\} = \max \{I_A, I_P\}.$$

d) If $N_{2R} > a, N_{2P} \leq a$, then

$$I^* = \max \{I_R, I_B\}.$$

Thus, the optimal productivity problem of a biosystem of the "predator-prey" type in the formulation given above can be fully investigated and solved.

3. Comparative Study of the Possible Existence of Stationary States with "Nondeteriorating" Types of Constraints for Two Different Models

The Kostitzin Model of a "Predator-Prey" Biosystem

The system of differential equations

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(\varepsilon_1 - \gamma_{12}N_2 - \gamma_{11}N_1) \\ \frac{dN_2}{dt} &= N_2(-\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2) \end{aligned} \right\}, \quad (33)$$

which describes a biocoenosis of the "predator-prey" type (the

Kostitzin Model) has two types of solutions.

If the condition

$$\begin{aligned} & [e_1\gamma_{22}(\gamma_{11} - \gamma_{22}) + e_2\gamma_{11}(\gamma_{12} + \gamma_{22})]^2 \leq \\ & \leq 4\gamma_{12}\gamma_{21}(e_1\gamma_{22} + e_2\gamma_{12})(e_1\gamma_{21} - e_2\gamma_{11}), \end{aligned} \quad (34)$$

is satisfied (weakly damped system), the number of "predators" and "prey" make damped oscillations over time, and the system has a non-zero singular point, a stable focus. The phase portrait of such a system is plotted in Fig. 17. /61

If condition (34) is not satisfied (strongly damped system) the numbers vary almost monotonically, and the system has a singular point, a stable node. The phase portrait for such a system is plotted in Fig. 18.

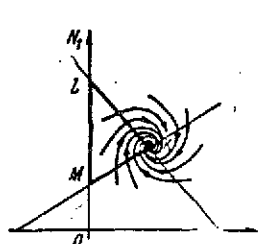


Fig. 17

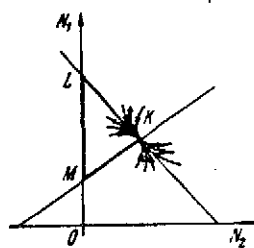


Fig. 18

Fig. 17. Phase portrait for system (22), when the point K is the stable focus

Fig. 18. Phase portrait for system (22), when the point K is the stable node.

In Section 1 of this chapter we studied in detail the problem of the stationary collection of the yield with a small fixed step, in the biogeocoenosis described by system (33). When we proved the existence of a stationary process we did not use the conditions which determine the type of singular point, it sufficed that it existed (this ensured that the feasible region Ω was bounded). In fact, the introduction of damping terms ensures both the existence of the single points and the boundedness of the region Ω and stability, which, in turn, ensures that the simplex Ω is not empty. Consequently, for a system with damping (Kostitzin Model) regardless of whether the number of "predators" or "prey" varies periodically or not, i.e., whether the system has for the singular point a focus or a node, it suffices for the stationary yield collection process with a fixed small step that the system be damped, i.e., that it have a singular point and that this point be stable.

The Volterra Model of A "Predator-Prey" Biosystem

We return to the problem of the optimal stationary yield collection in the biocoenosis, described by system (25). The

investigation of the stationary yield collection with a small fixed step in such a system reduces to a study of the following problem: to determine

$$\max_{N_1, N_2} \{I = c_1 N_1 (\varepsilon_1 - \gamma_{12} N_2) + c_2 N_2 (-\varepsilon_2 + \gamma_{21} N_1)\} \quad (35)$$

subject to the conditions

$$\left. \begin{array}{l} N_1 \geq 0, \quad dN_1 \geq 0 \\ N_2 \geq 0, \quad dN_2 \geq 0 \end{array} \right\} \quad (36)$$

Conditions (36) determine the feasible region Ω

$$\Omega: \left\{ \begin{array}{l} N_1 \geq \frac{\varepsilon_2}{\gamma_{21}} \\ 0 \leq N_2 \leq \frac{\varepsilon_1}{\gamma_{12}} \end{array} \right. \quad (37)$$

The region Ω which represents a halfstrip is plotted in Fig. 19.

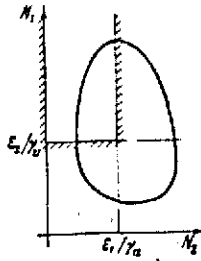


Fig. 19. The feasible region Ω determined by (37)

Setting the first derivatives of I with respect to N_1 and N_2 equal to zero, we see that the necessary conditions for the existence of the extremum are not satisfied at any point in the interior of the region Ω . Consequently, the function I does not have a maximum in the interior of Ω . We will investigate the behavior of I on the boundary of Ω . The problem reduces to the study of the following function of a single variable

$$I_{\Gamma} = \begin{cases} \varepsilon_1 c_1 N_1, & \text{if } \frac{\varepsilon_2}{\gamma_{21}} \leq N_1 \leq \infty \\ \frac{c_1 \varepsilon_1 \varepsilon_2}{\gamma_{21}} - \frac{c_1 \varepsilon_2 \gamma_{12}}{\gamma_{21}} \cdot N_2, & \text{if } 0 \leq N_2 \leq \frac{\varepsilon_1}{\gamma_{12}} \\ -\frac{c_2 \varepsilon_1 \varepsilon_2}{\gamma_{12}} + \frac{c_2 \varepsilon_1 \gamma_{21}}{\gamma_{12}} \cdot N_1, & \text{if } \frac{\varepsilon_2}{\gamma_{21}} \leq N_1 \leq \infty \end{cases}$$

It is easily seen that this function attains a maximum when $N_1 = \infty$, but an infinite value for the size of one of the species has no real meaning for us. Thus, we have shown that for the biocoenosis described by the Volterra Model, a stationary process with a small fixed step does not exist. But if we introduce into the Volterra Model even very weak damping (as Kostitzin did), the feasible region Ω becomes bounded, and this type of stationary collection problem may have a finite solution.

4. Stepsize, The Decision Parameter for the Stationary Yield Collection Process

It is interesting that an extension of the decision possibilities when the step in the process is also considered as a decision parameter makes it possible to obtain a stationary optimal yield collection process even in those models in which under more rigorous constraints (a fixed step specified in advance, a small stepsize, "non-deterioration" conditions, etc.), no stationary collection process existed.

Suppose that we are given a "predator-prey" biocoenosis described by a system of the form (25). As we have shown above when the step was specified in advance, it was not possible to have a stationary yield collection process in this case. We will now show that by choosing appropriate bounds for the phase variables, and mainly by choosing the step for the process, the optimal yield collection procedure can be made stationary in such a system.

We will assume that the number of "predators" and also the number of "prey" are bounded below, so that

$$\left. \begin{array}{l} N_1 \geq N_1^* \\ N_2 \geq N_2^* \end{array} \right\}. \quad (38)$$

Below we shall see that only one of these bounds is essential.

We formulate the problem of maximizing the yield collected in one step (local optimality)

$$\max \{I = c_1 \Delta N_1 + c_2 \Delta N_2\}, \quad (39)$$

where $\Delta N_1 = N_1^1 - N_1^0$, $\Delta N_2 = N_2^1 - N_2^0$ is the increment in the number of "prey" and "predators" in one step. In addition to the bounds (38), the variables N_1 and N_2 are constrained by the relations (26) determined from the equation for the cycle.

We will consider this problem geometrically. We will construct in the plane (N_1, N_2) a cycle, all points of which satisfy the second condition in (38); the first condition need not be satisfied. The cycle with the maximum amplitude constructed in this manner will be called the "maximum feasible cycle" and it will be denoted by Γ (Fig. 20). We write the expression for I in the form:

$$I = \{c_1 N_1^1 + c_2 N_2^1\} - \{c_1 N_1^0 + c_2 N_2^0\} = I_1 - I_0.$$

The expressions $I_1 = c_1 N_1^1 + c_2 N_2^1$ and $I_0 = c_1 N_1^0 + c_2 N_2^0$ are equations of straight lines in the plane (N_1, N_2) . The quantities I_1/c_1 and I_0/c_1 are the segments cut off by these lines on the N_1 axis. It is clear that I attains a maximum value when I_1 is a maximum and I_0 is a minimum. But since the variables N_1 and N_2 are related by the equation of the cycle, these straight lines must have common points with the cycle Γ . Clearly the straight line which is tangent to Γ above corresponds to the maximum value I_1 , and the line which is tangent to Γ below corresponds to the minimum value I_0 (see Fig. 20). We will call these lines the "maximum" and "minimum" tangent lines, respectively. Their equations are:

$$(I) \quad N_1 = \frac{I_1}{c_1} - \frac{c_2}{c_1} N_2 \quad (\text{"Maximum" tangent line})$$

$$(II) \quad N_1 = \frac{I_0}{c_1} - \frac{c_2}{c_1} N_2 \quad (\text{"Minimum" tangent line})$$

These are equations of two parallel lines with a negative slope $(c_1, c_2 \geq 0)$, where $\alpha = \arctg c_2/c_1$.

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The point A corresponds to the initial state of the system, and the point B to the final state. The time needed for the transition from the point A to the point B determines the step. The amount of yield collected is determined by the vector \overline{AB} , more precisely by its projection on the N_1 and N_2 axes. By construction among all possible values of the step and among all admissible states of the system, it is precisely this step and these limiting states which determine the maximum possible return from the yield collected.

The optimal stationary yield collection strategy will consist of the following: the system makes a transition into the state described by the point B, after which a certain amount of "prey" equal to $\delta N_1 = (N_1)_B - (N_1)_A$ and "predators" equal to $\delta N_2 = (N_2)_B - (N_2)_A$ are removed from the biocoenosis. This brings the system into the state represented by the point A, and then it

moves along the trajectory Γ to the point B. After the system makes a transition to the state represented by the point B, the process is repeated. The step is determined by the time needed for the transition of the system from point A to point B.

In Fig. 20 the greatest admissible cycle Γ lies above the straight line $N_1 = N_1^*$, and the bound on the number of "prey" has no effect on the nature of the optimal process. We will consider the situation when the line $N_1 = N_1^*$ intersects the greatest admissible cycle (Fig. 21). Here two cases can occur:

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a) The line $N_1 = N_1^*$ lies below the point A. This case does not differ from the case considered above. The bound on the number of "prey" has no effect on the optimal yield collection process.

b) The line $N_1 = N_1^*$ lies above the point A (see Fig. 21).

In this case the optimal stationary yield collection strategy consists of the following: the system makes a transition to state B, after which an amount of "prey" equal to $\delta N_1 = (N_1)_B - N_1^*$ is removed from the biocoenosis, and an amount of "predators" equal to $\delta N_2 = (N_2)_B - (N_2)_{A'}$. Thus, the system makes a transition to state A'. The transition can be described either by the vectors $\overrightarrow{A''B}$ and $\overrightarrow{A'A''}$, or by the vector $\overrightarrow{A'B} = \overrightarrow{A''B} + \overrightarrow{A'A''}$, which is clear from Fig. 21. Then no yield is collected in the time interval when the system makes the transition from A' to state B. This time is the unknown optimal step for the process. After the system arrives at point B the process is repeated again.

From everything that has been said it follows that the bound on the number of "prey" is not essential. Of course, in case b) the bound does have an effect on the yield which is collected, and the optimum trajectory contains points which lie on the boundary $N_1 = N_1^*$. But the optimum stationary yield collection strategy remains qualitatively the same. Only the bound on the number of "predators" has an effect on the greatest admissible cycle, which, in fact, determines the optimal trajectory.

In principle it is possible to construct a process in which a bound on the number of "predators" has no effect on the selection of the greatest admissible cycle, but in this case the decision, in addition to collecting the yield, i.e., removing from the biocoenosis a certain number of individuals of different species, must also include a method for introducing into the biocoenosis a certain number of individuals from certain species, i.e., instead of being passive it becomes active. Since these problems are beyond the

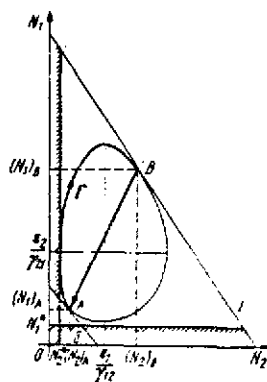


Fig. 20

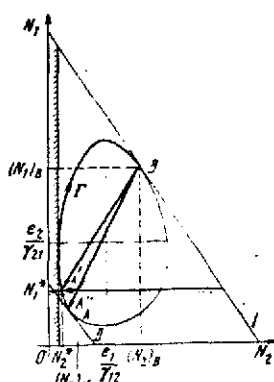


Fig. 21

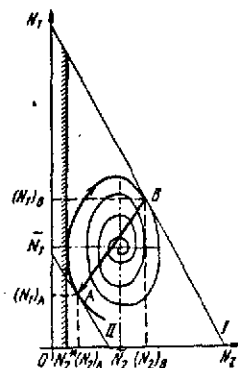


Fig. 22

Fig. 20. Stationary yield collection process in a Volterra system of the "predator-prey" type when the step in the process is considered as a decision parameter (bounds of the type (38))

Explanation in text

Fig. 21. Stationary yield collection in a Volterra "predator-prey" system when the step in the process is considered as a decision parameter (constraints of type "b")

Explanation in text

Fig. 22. Stationary yield collection in a "predator-prey" system described by equations (33), when the step in the process is the decision parameter

Explanation in text

scope of our study they will not be considered here.

In an analogous manner it is also possible to obtain the stationary yield collection process with the selected step for a biocoenosis described by a Kostitzin model of the form (33) where the number of "predators" and "prey" oscillate about a certain equilibrium (weakly damped system). Figure 22 gives the phase portrait for such a system. We will introduce a lower bound on the number of "predators"

$$N_2 > N_2^*$$

We will represent the phase trajectory of system (33) with the initial conditions

$$(N_1)_0 = \tilde{N}_1 = \frac{\epsilon_1 \gamma_{33} + \epsilon_3 \gamma_{21}}{\gamma_{21}^2 + \gamma_{11} \gamma_{23}}; \quad (N_2)_0 = N_2^*$$

in the plane (N_1, N_2) . We will call this trajectory the "greatest admissible" trajectory. By analogous reasoning we arrive at the following formulation of the optimal stationary yield collection strategy: The system makes a transition to the state B, after which an amount of "prey" equal to $\delta N_1 = (N_1)_B - (N_1)_A$ and an amount of "predators" equal to $\delta N_2 = (N_2)_B - (N_2)_A$ are removed from it. Thereby the system makes the transition to state A. Then the system moves along the trajectory from point A to point B. No yield is collected in this time period. When the system arrives at point B, the process is repeated again. The step is determined by the time necessary for the transition of the system from state A to state B. It is clear that the yield collection strategies, using the stepsize as a decision parameter in biosystems described by the Volterra and Kostitzin models, do not differ in principle.

5. Stationary Yield Collection Process for Models of More Complex Biosystems

We will consider a special case of a biogeocoenosis model consisting of n species (Kostitzin, 1937). We will assume that the graph of the trophic relations in the biogeocoenosis is linear, i.e., that the i -th species feeds only on the $(i-1)$ -th species, which in turn is the food for the $(i+1)$ -th species, etc. The last n -th species is not eaten by any other species. Such biogeocoenosis is described by the following system of differential equations:

$$\frac{dN_i}{dt} = N_i \left(\epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right), \quad i = 1, 2, \dots, n, \quad (40)$$

where $\gamma_{ij} = -\gamma_{ji}$ ($i \neq j$), $\gamma_{ii} \neq 0$, $\gamma_{i, i+1} \neq 0$, $\gamma_{i, i-1} \neq 0$. For all other (i, j) $\gamma_{ij} = 0$. The coefficients $\epsilon_1 > 0$, $\epsilon_i < 0$ ($i = 2, 3, \dots, n$).

Qualitative studies of system (40) have shown that the stationary point of such biogeocoenosis is always asymptotically stable, i.e., there are no undamped cycles in such a system. The solutions of the system represent either damped oscillations about the stationary point or converge monotonically to it.

We will seek the stationary yield collection process in such system. Since this system has a stable singular point, we have reason to believe that for this system a stationary yield collection process with a small fixed step exists. The problem can be studied as a nonlinear programming problem.

The criterion function has the form

$$I = \sum_{i=1}^n c_i N_i \left(e_i - \sum_{j=1}^n \gamma_{ij} N_j \right). \quad (41)$$

(the increment in the biomass of each species in one step is removed).

We assume that the step is sufficiently small so that the increment in the biomass is linear over time. The step is selected per unit time.

The "nondeterioration" conditions for biosystem (40) will be written in the following form:

$$\left. \begin{aligned} N_i &\geq 0 \\ e_i - \sum_{j=1}^n \gamma_{ij} N_j &\geq 0 \end{aligned} \right\}. \quad (42)$$

These constraints define the feasible region Ω . If the criterion function (41) is strictly concave in the region Ω , the maximum of I exists and is unique.

We will consider the optimal productivity problem for biosystem (40) when $n = 3$. The mathematical model of this biosystem has the form:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1 (e_1 - \gamma_{12} N_2 - \gamma_{11} N_1) \\ \frac{dN_2}{dt} &= N_2 (-e_2 + \gamma_{21} N_1 - \gamma_{23} N_3 - \gamma_{22} N_2) \\ \frac{dN_3}{dt} &= N_3 (-e_3 + \gamma_{32} N_2 - \gamma_{33} N_3) \end{aligned} \right\}. \quad (43)$$

Biologically the given system can be represented as follows: The first species is vegetation, the second species are herbivorous animals and the third species are predators who feed on the

herbivorous animals.

We must find the maximum total yield per unit time, i.e., the maximum of the criterion function (41) when $i = 1, 2, 3$ and satisfy at the same time the following constraints:

$$\left. \begin{aligned} N_1, N_2, N_3 &\geq 0 \\ \varepsilon_1 - \gamma_{11}N_1 - \gamma_{12}N_2 &\geq 0 \\ -\varepsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2 - \gamma_{23}N_3 &\geq 0 \\ -\varepsilon_3 + \gamma_{32}N_2 - \gamma_{33}N_3 &\geq 0 \end{aligned} \right\} \quad (44)$$

The stationary point of I is determined from the system:

$$\left. \begin{aligned} \varepsilon_1 c_1 - 2\gamma_{11}c_1 N_1 + (c_2 - c_1)\gamma_{21}N_2 &= 0 \\ -\varepsilon_2 c_2 + (c_2 - c_1)\gamma_{21}N_1 - 2\gamma_{22}c_2 N_2 + (c_3 - c_2)\gamma_{23}N_3 &= 0 \\ -\varepsilon_3 c_3 + (c_3 - c_2)\gamma_{23}N_2 - 2\gamma_{33}c_3 N_3 &= 0 \end{aligned} \right\} \quad (45)$$

Here we assume that $\gamma_{12} = \gamma_{21}$, $\gamma_{23} = \gamma_{32}$. The coordinates of the stationary point of the criterion function are

$$\begin{aligned} N_1^0 &= \frac{2\varepsilon_2\gamma_{33}c_2c_3 + \varepsilon_1\gamma_{23}^2(c_3 - c_2)^2c_1 - \gamma_{22}\varepsilon_3\gamma_{23}(c_3 - c_2)c_2 - 4\varepsilon_1\gamma_{21}\gamma_{33}c_1c_2c_3}{2[\gamma_{11}\gamma_{23}^2(c_3 - c_2)^2c_1 + \gamma_{21}^2\gamma_{33}(c_2 - c_1)^2c_3 - 4\gamma_{11}\gamma_{21}\gamma_{33}c_1c_2c_3]}, \\ N_2^0 &= \frac{2[2\varepsilon_3\gamma_{11}\gamma_{33}c_1c_2c_3 + \varepsilon_2\gamma_{11}\gamma_{23}(c_3 - c_2)c_1c_3 - \varepsilon_1\gamma_{21}\gamma_{33}(c_2 - c_1)c_1c_3]}{2[\gamma_{11}\gamma_{23}^2(c_3 - c_2)^2c_1 + \gamma_{21}^2\gamma_{33}(c_2 - c_1)^2c_3 - 4\gamma_{11}\gamma_{21}\gamma_{33}c_1c_2c_3]}, \\ N_3^0 &= \frac{4\varepsilon_2\gamma_{11}\gamma_{22}c_1c_2c_3 + 2\varepsilon_3\gamma_{11}\gamma_{23}(c_3 - c_2)c_1c_2 - \varepsilon_1\gamma_{21}\gamma_{23}(c_3 - c_2)(c_2 - c_1) - \varepsilon_3\gamma_{21}^2c_3(c_2 - c_1)^2}{2[\gamma_{11}\gamma_{23}^2(c_3 - c_2)^2c_1 + \gamma_{21}^2\gamma_{33}(c_2 - c_1)^2c_3 - 4\gamma_{11}\gamma_{21}\gamma_{33}c_1c_2c_3]} \end{aligned}$$

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A necessary and sufficient condition that the criterion function I have a maximum at the point (N_1^0, N_2^0, N_3^0) , in the region (44) is that the quadratic form (41) be negative-definite, i.e., that the function I be concave in the neighborhood of this point. The conditions that the quadratic form be negative-definitive imply that

$$\left. \begin{aligned} 4\gamma_{11}\gamma_{22}c_1c_2 - (c_2 - c_1)^2\gamma_{21}^2 &> 0 \\ \gamma_{11}\gamma_{23}^2(c_3 - c_2)^2c_1 + \gamma_{21}^2\gamma_{33}(c_2 - c_1)^2c_3 - 4\gamma_{11}\gamma_{21}\gamma_{33}c_1c_2c_3 &< 0 \end{aligned} \right\}.$$

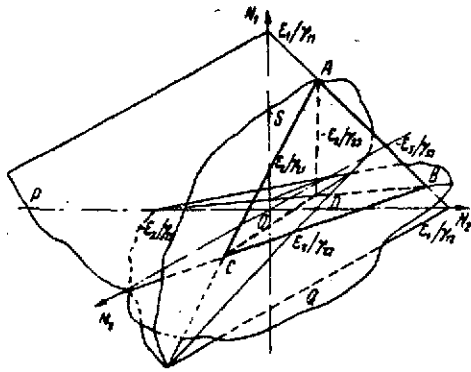


Fig. 23. Feasible region Ω (the tetrahedron ABCD) determined by (44)

A necessary and sufficient condition that the stationary point (N_1^0, N_2^0, N_3^0) be a point at which I is a maximum, is that the internal parameters of system (43) and the corresponding costs c_1, c_2, c_3 satisfy the following system of inequalities:

$$\left\{ \begin{array}{l} 4\gamma_{11}\gamma_{22}c_1c_2 - (c_2 - c_1)^2\gamma_{21}^2 > 0 \\ \gamma_{11}\gamma_{22}^2(c_3 - c_2)^2c_1 + \gamma_{21}^2\gamma_{33}(c_2 - c_1)^2c_3 - 4\gamma_{11}\gamma_{22}\gamma_{33}c_1c_2c_3 < 0 \\ e_1\gamma_{22}^2c_1(c_3 - c_2)^2 + e_3\gamma_{21}\gamma_{23}c_3(c_3 - c_2)(c_2 - c_1) + 2e_2\gamma_{21}\gamma_{33}c_2c_3(c_2 - c_1) - \\ \quad - 4e_1\gamma_{22}\gamma_{33}c_1c_2c_3 < 0 \\ 2\gamma_{11}\gamma_{33}e_2c_3 + \gamma_{11}\gamma_{23}e_3(c_3 - c_2) - \gamma_{21}\gamma_{33}e_1(c_2 - c_1) < 0 \\ 4e_3\gamma_{11}\gamma_{22}c_1c_2c_3 + 2e_2\gamma_{11}\gamma_{23}c_1c_2(c_3 - c_2) - \gamma_{21}\gamma_{23}e_1c_1(c_3 - c_2)(c_2 - c_1) - \\ \quad - e_3\gamma_{21}^2c_3(c_2 - c_1)^2 < 0, \end{array} \right.$$

and that the point (N_1^0, N_2^0, N_3^0) lie in the interior of the region /69 bounded by the planes:

$$\begin{array}{ll} e_1 - \gamma_{12}N_2 - \gamma_{11}N_1 = 0, & (P) \\ -e_2 + \gamma_{21}N_1 - \gamma_{22}N_2 - \gamma_{22}N_2 = 0, & (Q) \\ -e_3 + \gamma_{32}N_2 - \gamma_{33}N_3 = 0. & (S) \end{array}$$

We will construct in the space (N_1, N_2, N_3) the region Ω bounded by the planes P, Q and S. In the process we will take into account the condition

$$e_1\gamma_{21} > e_2\gamma_{11}.$$

for the stability of the biosystem.

It is easily seen that a necessary condition that the stationary point (N_1^0, N_2^0, N_3^0) lie in the interior of the region Ω is that the coordinates of this point satisfy the inequalities:

$$\left. \begin{aligned} 0 < N_1^0 &< \frac{e_1 \gamma_{22} - e_2 \gamma_{12}}{\gamma_{11} \gamma_{22}} \\ \frac{e_2}{\gamma_{22}} < N_2^0 &< \frac{e_1}{\gamma_{12}} \\ 0 < N_3^0 &< \frac{e_1 \gamma_{22} - e_2 \gamma_{12}}{\gamma_{12} \gamma_{22}} \end{aligned} \right\}.$$

If one or more of these inequalities are not satisfied, the stationary point (N_1^0, N_2^0, N_3^0) of the criterion function does not lie in the interior of the region Ω , and the maximum value of I must be sought on the boundaries of the region Ω (Fig. 23).

The optimization of the productivity of biosystems with $n > 3$ is the same in principle as long as the system contains no cycles and the feasible region for the criterion function is bounded.

CHAP. V. OPTIMIZATION PROBLEMS RELATED TO CHANGES IN THE TROPHIC STRUCTURE OF BIOGEOCOENOSES

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1. Dynamic Equations for Biological Systems

A very large class of biological systems (biogeocoenoses), populations, photosynthesis systems, enzymatic reaction systems in the living organism) can be described by the following dynamic equations:

$$\frac{dN_i}{dt} = a_i + \sum_{j=1}^n e_{ij} N_j - N_i \sum_{j=1}^n \gamma_{ij} N_j, \quad i=1, 2, \dots, n. \quad (46)$$

Here N_i are the phase variables of the dynamic system (46). These can either be the number of species in a BGC, or the sizes of population age groups, or concentrations of chemical substances in an enzyme system. Since we study BGC models, we shall mean by N_i the number of individuals in the i -th group having a certain i -th characteristic (i -th species, i -th age group, etc.). Then the a_i are quantities which characterize the emigration or immigration of individuals in the i -th group, e_{ii} is the natural growth

coefficient in the i -th group. The expression $\epsilon_{ij}N_j$ ($i \neq j$) characterizes the mutual transformation of individuals and associated transitions between groups, for example, when N_j are the sizes of the age groups in one species. The quantities γ_{ii} take into account the effect of limiting factors within the species (intra-specific competition, limited area, etc.). The quantities γ_{ij} ($i \neq j$) characterize the interaction between individuals from different groups (interspecific competition, symbiosis, parasitism, etc.).

2. Simplest Dynamic Model of a Biogeocoenosis

The simplest BGC model is the dynamic system in which the phase variables are the number of species which make up the BGC. Since BGC is in a certain sense a closed system, we can assume that no migration occurs between neighboring BGC, so that $\alpha_i = 0$. The effect of the environment is taken into account by the parameters γ_{ij} . It is assumed that the individuals of one species are completely identical (they do not differ by sex, age, size, etc.) and they cannot reproduce individuals of a different species. Therefore, $\epsilon_{ij} = 0$ ($i \neq j$). Then (46) is written in the form

$$\frac{dN_i}{dt} = \left(\epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right) N_i, \quad i = 1, 2, \dots, n. \quad (47)$$

This system was studied by Volterra and V. A. Kostitzin. System (47) has 2^n stationary equilibrium states: /71

a) One state of the type

$$\tilde{N}_1 = \tilde{N}_2 = \dots = \tilde{N}_n = 0.$$

This state is stable if all natural growth coefficients are negative.

$$\epsilon_i < 0, \quad i = 1, 2, \dots, n;$$

b) n states of the type

$$\begin{aligned} \tilde{N}_1 = \dots = \tilde{N}_{i-1} = 0; \quad \tilde{N}_i = \frac{\epsilon_i}{\gamma_{ii}}; \\ \tilde{N}_{i+1} = \dots = \tilde{N}_n = 0, \quad i = 1, 2, \dots, n. \end{aligned}$$

These states are stable if

$$\varepsilon_i > 0, \quad \gamma_{ii} > 0, \quad \varepsilon_i \gamma_{ii} < \varepsilon_i \gamma_{ij}, \\ j = 1, 2, \dots, i-1, i+1, \dots, n;$$

c) $\frac{n(n-1)}{2}$ states

$$\tilde{N}_1 = \frac{\varepsilon_1 \gamma_{22} - \varepsilon_2 \gamma_{21}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}; \quad \tilde{N}_2 = \frac{\varepsilon_2 \gamma_{11} - \varepsilon_1 \gamma_{12}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}; \quad \tilde{N}_3 = \dots = \tilde{N}_n = 0;$$

d) and, finally, there exists a stationary state in which all species are represented. This state is determined by solving the following linear system

$$\sum_{j=1}^n \gamma_{ij} N_j = \varepsilon_i, \quad i = 1, 2, \dots, n. \quad (48)$$

We can determine in the usual manner under which constraints on the parameters of system (47) the solution (48) is stable.

Only this state has no \tilde{N}_i values which are zero. In any other stationary state (47) there will necessarily be zero \tilde{N}_i values. If the components of the vector $\tilde{N}(\tilde{N}_1, \tilde{N}_2, \dots, \tilde{N}_n)$ which vanish are known, the nonzero components are found by solving the reduced system (48), in which the rows and columns which correspond to the numbers of the zero components of the vector have been eliminated.

3. Concept of the Trophic Structure and the Trophic Graph of a Biogeocoenosis

Above, without going into great detail (section 5, Chap. IV) we used the concept of the trophic graph or the graph of trophic relations. Here we shall study this concept in greater detail.

The BGC model which was given in the previous section is a dynamic system, the behavior of which is completely determined by the vector of initial conditions $\vec{N}_0 \{(N_1)_0, (N_2)_0, \dots, (N_n)_0\}$, the vector $\vec{\varepsilon}(\varepsilon_1, \varepsilon_2, \dots, \varepsilon_n)$ and the matrix $\Gamma(\gamma_{ij})_{i,j=1,2,\dots,n}$ where the stationary stable states of the BGC depend only on $\vec{\varepsilon}$ and Γ . If the ε_i are parameters which are predominantly determined by belonging to a class of species, the elements γ_{ij} of the matrix characterize both the intraspecific competitive relations ($i = j$)

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as well as the interspecific competition ($i \neq j$), i.e., essentially they determine, together with the ϵ_i , the BGC structure. We note that the parameters γ_{ij} may characterize not only the trophic relations but also other types of relations. Therefore, we shall use the concept "trophic" in the generalized sense, and include in it also symbiosis, interspecific competition for food and parasitism, etc.

We shall consider simple examples of BGC with different trophic structures.

a) Suppose that the BGC consists of a single species population and its surrounding environment. If enough food and other factors necessary to sustain life are available in the environment, the population size (N) increases without limit, so that

$$\frac{dN}{dt} = \alpha N,$$

where $N(t_0) = N_0$ is the initial population size, and $\alpha > 0$ is the natural growth coefficient for the population. The propagation of such populations is only limited by the surrounding environment and by intraspecific competition which begins to manifest itself when the number of competing individuals within the species is large so that

$$\frac{dN}{dt} = \alpha N - \gamma N^2.$$

where

$$\lim_{t \rightarrow \infty} N = \frac{\alpha}{\gamma}.$$

Here $\gamma \geq 0$ is determined both by the conditions in the external environment as well as the character of the competition within the species. The species whose population size in the BGC is described in such a manner, will be called "prey" of order zero, and will be denoted graphically as the zero node in the graph (see Fig. 24).

b) Suppose that the BGC consists of two species, one of which is "prey" of order zero, which serves as food for the second species, the "predator" of order one. A system of this type is described by the equations

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(\epsilon_1 - \gamma_{12}N_2 - \gamma_{11}N_1) \\ \frac{dN_2}{dt} &= N_2(\epsilon_2 + \gamma_{21}N_1 - \gamma_{22}N_2) \end{aligned} \right\}.$$

If N_1 is the number of "prey" and N_2 the number of "predators" we must have $\epsilon_1 > 0$; $\epsilon_2 < 0$; $\gamma_{11}, \gamma_{22} \geq 0$; $\gamma_{12} > 0$; $\gamma_{21} < 0$. On what basis are the signs of these coefficients chosen? If there is no "predator" we have case a) where the number of "prey" is only limited by the surrounding environment. Therefore, $\epsilon_1 > 0$, $\gamma_{11} \geq 0$. If there are "predators" the rate of growth of the "prey" naturally decreases. Therefore $\gamma_{12} > 0$. If there are no "prey" then the "predators" who are deprived of food will die out at the rate $\epsilon_2 N_2$ so that we must have $\epsilon_2 < 0$. The appearance of "prey" is accompanied by an increased rate of growth of the "predators." Therefore $\gamma_{21} < 0$. An increase in the number of "predators" leads to intensified competition within the species, and consequently to a drop in the rate of growth of the "predators" so that $\gamma_{22} \geq 0$.

We will represent this in the form of an oriented graph (Fig. 24).

Subsequently when we represent the trophic BGC structure, we will use a graph which is constructed according to the following rules:

1) The nodes will denote the species of which the BGC is made up. Naturally the number of nodes is equal to the number of species. All nodes are divided into two types: "prey" of order zero, and "predators" of all orders.

2) An arc of the graph, which connects two nodes, indicates the presence of a generalized trophic relation between the species which correspond to these nodes.

3) If the interaction between two species is such that the biomass of the first species stimulates an increment in the biomass of the second species, and the biomass of the second species suppresses the growth in the biomass of the first species, the arc is oriented from the first node to the second node. The simplest case of such interaction is when individuals in the first species serve as food for individuals in the second species.

4) If the interaction between two species is such that the increment in the biomass of both species is either stimulated simultaneously (the species form a coalition) or is suppressed simultaneously (competition between two species for the same

food, area, etc.) the arc which connects the two corresponding nodes is not oriented. Nevertheless, we shall distinguish two types of arcs, arcs which connect species in a coalition and arcs which connect competing species.

Figure 25 gives an example of a trophic graph for a certain BGC. In it the first and second species are "prey" of order zero which are related among themselves by competitive relations. The third and fourth species are "predators" of order one which form a coalition. Individuals in the third species feed on individuals of the first and second species (without preference of any kind) and individuals in the fourth species feed only on individuals of the second species. The fifth species is a "predator" of order two, which feeds on individuals of the third species.

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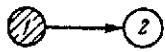


Fig. 24

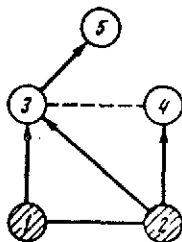


Fig. 25

Fig. 24. Linear oriented graph of a "predator (2) - prey" (1) system

Fig. 25. Trophic graph of a BGC model

Explained in text

4. A Dynamic System Determined by the Trophic Graph

The number ϵ can be made to correspond to each node of the trophic graph, where for the nodes corresponding to the "prey" of order zero $\epsilon > 0$, and for all remaining nodes $\epsilon < 0$. In the first case ϵ characterizes the natural growth in the number of "prey" under optimal conditions for its development; in the second case it denotes the natural mortality of the "predators" in the complete absence of food.

To each arc of the graph (i, j) we can make correspond the numbers γ_{ij} and γ_{ji} ($i \neq j$) which characterize the effect of a particular type of interaction between the i -th and j -th species on the size of the i -th (γ_{ij}) and j -th (γ_{ji}) species. If the arc is oriented from i to j , then $\gamma_{ij} > 0$, and $\gamma_{ji} < 0$. If the arc is not oriented, then for a coalition, both γ_{ij} and γ_{ji} are negative, and in the presence of competition they are positive. If the nodes are not connected, the corresponding $\gamma_{ij} = \gamma_{ji} = 0$.

The trophic BGC graph has no arcs which lead from a node to the same node. These arcs correspond to the relations within one species. The numbers γ_{ii} which correspond to these arcs can be

associated directly with the nodes of the graph, which allows us not to consider the arcs themselves. Thus, to each i -th node corresponds the number γ_{ii} . Since the relations within the species reduce mainly to competition within the species, $\gamma_{ii} \geq 0$.

For the graph shown in Fig. 25, the vector \vec{e} and the matrix Γ will have the form

$$\vec{e} = \begin{pmatrix} e_1 \\ e_2 \\ -e_3 \\ -e_4 \\ -e_5 \end{pmatrix}; \quad \Gamma = \begin{pmatrix} \gamma_{11} & \gamma_{12} & \gamma_{13} & 0 & 0 \\ \gamma_{21} & \gamma_{22} & \gamma_{23} & \gamma_{24} & 0 \\ -\gamma_{31} & -\gamma_{32} & \gamma_{33} & -\gamma_{34} & \gamma_{35} \\ 0 & -\gamma_{42} & -\gamma_{43} & \gamma_{44} & 0 \\ 0 & 0 & -\gamma_{53} & 0 & \gamma_{55} \end{pmatrix}$$

In this case for convenience all e_i and γ_{ij} are assumed to be positive.

The dynamic system is constructed from the vector \vec{e} and the matrix Γ : /75

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(e_1 - \gamma_{11}N_1 - \gamma_{12}N_2 - \gamma_{13}N_3) \\ \frac{dN_2}{dt} &= N_2(-e_2 - \gamma_{21}N_1 - \gamma_{22}N_2 - \gamma_{23}N_3 - \gamma_{24}N_4) \\ \frac{dN_3}{dt} &= N_3(-e_3 + \gamma_{31}N_1 + \gamma_{32}N_2 - \gamma_{33}N_3 + \gamma_{34}N_4 - \gamma_{35}N_5) \\ \frac{dN_4}{dt} &= N_4(-e_4 + \gamma_{42}N_2 + \gamma_{43}N_3 - \gamma_{44}N_4) \\ \frac{dN_5}{dt} &= N_5(-e_5 + \gamma_{53}N_3 - \gamma_{55}N_5) \end{aligned} \right\}.$$

or

$$\frac{d \ln \vec{N}}{dt} = \vec{e} - \Gamma \vec{N},$$

where

$$\ln \vec{N} (\ln N_1, \ln N_2, \dots, \ln N_5).$$

In exactly the same manner it is possible to construct from any trophic graph the corresponding dynamic system which is the mathematical model for the given BGC.

5. Optimization of the Trophic Structure

If all n species coexist in the BGC, their sizes in the stationary state are determined from the equation.

$$\vec{N} = \Gamma^{-1} \cdot \vec{e}. \quad (49)$$

We can formulate the following optimality problem: what must be the trophic BGC structure which is basically determined by the matrix Γ in order that the total value of the BGC be a maximum? By the total value of the BGC we shall mean the sum of biomasses whose value we estimated in a certain way or the number of all individuals in the BGC in the stationary state. In other words we must maximize the following functional ($c_i > 0$ is the unit cost for the biomass (individual) of the i -th species):

$$I = \sum_{i=1}^n c_i \tilde{N}_i = (\vec{c} \cdot \vec{\tilde{N}}) = (\vec{c} \cdot \Gamma^{-1} \vec{e}) \quad (50)$$

over the γ_{ij} , which can be constrained in various ways.

We will consider these constraints in greater detail. First, we have natural constraints related to the signs of the γ_{ij} ; evidently it is not possible to change the type of interrelations both among individuals in different species as well as among individuals within one species, only their degree can be changed by changing the absolute values of the γ_{ij} .

Second, the absolute values of the γ_{ij} can also be constrained /76 in certain ways. These constraints arise both from the stability requirement for the stationary state, and also from the limited possibilities of changing the quantities themselves.

Constraints of the first type represent a certain n^2 -dimensional octant in the n^2 -dimensional space of the γ_{ij} (the dimension of the octant can be smaller when certain $\gamma_{ij} = 0$).

Constraints of the second type represent in this octant a certain feasible region of the values of the variables γ_{ij} . Thus, our optimization problem reduces to finding the maximum of a function of n^2 variables over the region Ω determined by the constraints

on the γ_{ij} . If the system

$$(\det) \cdot \frac{\partial I}{\partial \gamma_{kl}} = \sum_{i=1}^n \sum_{j=1}^n c_i e_j \left(\frac{\partial A_{ij}}{\partial \gamma_{kl}} - \frac{A_{kl}}{\det} \right) = 0, \quad k, l = 1, 2, \dots, n. \quad (51)$$

where \det is the determinant of the matrix Γ

$\det \neq 0$, and

A_{ij} is the cofactor of the (i, j) -th element of the determinant has solutions $\{\gamma_{ij}^*\} \in \Omega$ and in addition to this the $n^2 \times n^2$ matrix R with the elements

$$\frac{\partial^2 I}{\partial \gamma_{kl} \partial \gamma_{sm}}, \quad k, l, s, m = 1, 2, \dots, n$$

is negative-definite, then

$$I(\gamma_{ij}^*) = \max_{\gamma_{ij} \in \Omega} I.$$

If any of these conditions is not satisfied, the optimum solution $\{\gamma_{ij}^*\}$ in which we are interested will always lie on the boundary of the feasible region Ω .

It is clear that when the number of species is large and when the trophic structure is complex, this problem can only be solved numerically. We will consider simpler but also clearer models.

6. Optimal Structure of a System Consisting of Two Species

We will consider a BGC consisting of two species of individuals and the surrounding environment. Suppose that the species either compete among themselves for the same food, or that one of them are the "predator" and the other the "prey." The model of such a system is described by the equations

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1(e_1 - \gamma_{11}N_1 - \gamma_{12}N_2) \\ \frac{dN_2}{dt} &= N_2(e_2 - \gamma_{21}N_1 - \gamma_{22}N_2) \end{aligned} \right\}, \quad (52)$$

where in the first case $\epsilon_1, \epsilon_2 > 0, \gamma_{11}, \gamma_{22}, \gamma_{12}, \gamma_{21} > 0$, and in the second case $\epsilon_1 > 0, \epsilon_2 < 0, \gamma_{11}, \gamma_{22}, \gamma_{12} > 0, \gamma_{21} < 0$.

Their stationary sizes are determined from the formula:

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$$\tilde{N}_1 = \frac{\epsilon_1 \gamma_{22} - \epsilon_2 \gamma_{12}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}; \quad \tilde{N}_2 = \frac{\epsilon_2 \gamma_{11} - \epsilon_1 \gamma_{21}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}.$$

This solution is strictly positive and stable, if

$$\epsilon_1 \gamma_{22} > \epsilon_2 \gamma_{12}, \quad (53)$$

$$\epsilon_2 \gamma_{11} > \epsilon_1 \gamma_{21}. \quad (54)$$

Conditions (53) specify certain natural constraints in four dimensional space $\{\gamma\}$.

The function which is maximized has the form

$$I = \frac{c_1 (\epsilon_1 \gamma_{22} - \epsilon_2 \gamma_{12}) + c_2 (\epsilon_2 \gamma_{11} - \epsilon_1 \gamma_{21})}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}. \quad (55)$$

Equating to zero the first derivatives of this function with respect to all γ gives:

$$\left. \begin{aligned} c_1 \epsilon_1 &= I^* \gamma_{11}^*; & c_2 \epsilon_1 &= I^* \gamma_{12}^* \\ c_1 \epsilon_2 &= I^* \gamma_{21}^*; & c_2 \epsilon_2 &= I^* \gamma_{22}^* \end{aligned} \right\}. \quad (56)$$

Here I^* is the value of the function at the point $(\gamma_{11}^*, \gamma_{22}^*, \gamma_{12}^*, \gamma_{21}^*)$ at which its first derivatives vanish.

It is easily seen that in the "predator-prey" case the system (56) does not have a solution in the feasible region, since $I^*, c_2, \gamma_{22}^* > 0$, and $\epsilon_2 < 0$, so that $c_2 \epsilon_2 < I^* \gamma_{22}^*$.

Let us pass on to the case of two species which compete for food. We will show that also in this case system (56) has no solution in the feasible region. From (56) we will have

$$\gamma_{12}^* = \frac{c_2}{c_1} \gamma_{11}^*; \quad \gamma_{21}^* = \frac{\epsilon_2}{\epsilon_1} \gamma_{11}^*; \quad \gamma_{22}^* = \frac{c_2 \epsilon_2}{c_1 \epsilon_1} \gamma_{11}^*. \quad (57)$$

Substituting (57) in (53) we obtain:

$$\begin{aligned} \varepsilon_1 \frac{c_1 \cdot \varepsilon_3}{c_1 \cdot \varepsilon_1} - \varepsilon_2 \frac{c_2}{c_1} \gamma_{11}^* &> 0, \\ \varepsilon_3 \gamma_{11}^* - \varepsilon_1 \frac{\varepsilon_3}{\varepsilon_1} \gamma_{11}^* &> 0, \end{aligned}$$

which is not possible. The point $(\gamma_{11}^*, \gamma_{22}^*, \gamma_{12}^*, \gamma_{21}^*)$ lies on the boundary of the stability region beyond the boundaries of the feasible region determined both by the inequalities (53) and by other constraints.

It follows from what was shown above that the function I does not have an extremum in the region Ω . It takes on its maximum value on the boundary of the region. But since the region Ω is an open set which does not include its boundary, we must study the behavior of I in some neighborhood of points on the boundary. /78

We will determine the region Ω for the case of two competing species. For simplicity we let $\gamma_{12} = \gamma_{21}$. Since in three-dimensional space $\{\gamma_{11}, \gamma_{12}, \gamma_{22}\}$, $\gamma_{11}, \gamma_{22}, \gamma_{12} > 0$, the open region Ω always lies in the positive octant, and it is bounded by the coordinate planes. On the other hand conditions (53, 54) show that Ω is also bounded by two other planes. In addition there are other possible types of constraints which we will not consider for the time being. The region Ω

$$\Omega: \begin{cases} \gamma_{11}, \gamma_{12}, \gamma_{22} > 0 \\ \gamma_{11} > \frac{\varepsilon_1}{\varepsilon_2} \gamma_{12}; \quad \gamma_{22} > \frac{\varepsilon_2}{\varepsilon_1} \gamma_{12} \end{cases} \quad (58)$$

is plotted in Fig. 26. It represents the interior of the trihedral angle with the vertex at the coordinate origin.

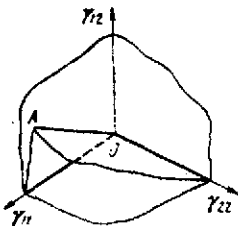


Fig. 26. Feasible region Ω determined by (58)

Since I attains its maximum value on the boundary Ω which is not part of the feasible region, we must study the behavior of I

in some neighborhood of the boundary points.

However, we can proceed more simply: we will include in the feasible region all boundary points at which I is not infinite. These points are all points which lie on the faces of the trihedral angle, except the edges OY_{11} and OY_{22} and O and possibly the edge OA . But the points which lie in some neighborhood of these edges are of the greatest interest to us.

At all points on the edges OY_{11} and OY_{22} (except possibly the coordinate origin) the function I takes on infinite values, since the denominator in (55) is zero at these points whereas the numerator is different from zero. For points on the edge OA , the denominator and numerator in (55) vanish simultaneously. Hence we must resolve the indeterminacy.

Let us calculate the values of I on the plane $Y_{12} = 0$:

$$I_{Y_{12}} = \frac{c_1 e_1}{\gamma_{11}} + \frac{c_2 e_2}{\gamma_{22}}. \quad (59)$$

On the plane $e_1 Y_{22} - e_2 Y_{12} = 0$ which intersects the OY_{11} axis

$$I_{Y_{12}} = \frac{c_2 e_2}{\gamma_{22}} = \frac{c_1 e_1}{\gamma_{12}}. \quad (60)$$

On the plane $e_2 Y_{11} - e_1 Y_{12} = 0$ which intersects the OY_{22} axis

$$I_{Y_{12}} = \frac{c_1 e_1}{\gamma_{11}} = \frac{c_2 e_2}{\gamma_{12}}. \quad (61)$$

Comparing the values (59), (60) and (61), we see that I takes on the greatest values on the plane $Y_{12} = 0$. If this plane is not in the feasible region, selecting the smallest possible Y_{12} is optimal. /79

It is of interest to study the behavior of the basic model system (52) at points on the edge OA on the boundary of the stability region. At these points

$$\gamma_{11} = \frac{e_1}{e_2} \gamma_{12}; \quad \gamma_{22} = \frac{e_2}{e_1} \gamma_{12}.$$

Substituting these values in (52) we obtain:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= N_1 \left[\varepsilon_1 - \gamma_{12} \left(\frac{\varepsilon_1}{\varepsilon_2} N_1 + N_2 \right) \right] \\ \frac{dN_2}{dt} &= \frac{\varepsilon_2}{\varepsilon_1} N_2 \left[\varepsilon_1 - \gamma_{12} \left(\frac{\varepsilon_1}{\varepsilon_2} N_1 + N_2 \right) \right] \end{aligned} \right\} \quad (62)$$

In this case we have a set of stationary points which lie on the line

$$\tilde{N}_1 = \frac{\varepsilon_2}{\gamma_{12}} - \frac{\varepsilon_2}{\varepsilon_1} \tilde{N}_2 \quad (63)$$

and all of them are stable. The equation of the trajectory in phase space (N_1, N_2) can be written in the form

$$N_1 = c N_2^{\frac{\varepsilon_1}{\varepsilon_2}}.$$

The phase portrait of system (62) is plotted in Fig. 27.

$$\begin{aligned} \text{I. } N_1 &= \frac{\varepsilon_2}{\gamma_{12}} - \frac{\varepsilon_2}{\varepsilon_1} N_2, \\ \text{II. } N_1 &= c N_2^{\frac{\varepsilon_1}{\varepsilon_2}}. \end{aligned}$$

The function I takes on the following values on the line (63): /80

$$I(\tilde{N}_1) = \tilde{N}_1 \left(c_1 - \frac{\varepsilon_1}{\varepsilon_2} c_2 \right) + \frac{c_2 \varepsilon_1}{\gamma_{12}}. \quad (64)$$

If $c_1 \varepsilon_2 < c_2 \varepsilon_1$, then $\max I(\tilde{N}_1)$ is attained when $\tilde{N}_1 = 0$, and it is equal to

$$I_2^* = \frac{c_2 \varepsilon_1}{\gamma_{12}}.$$

Since on OA $\frac{\varepsilon_1}{\gamma_{12}} = \frac{\varepsilon_2}{\gamma_{21}}$, $I_2^* = \frac{c_2 \varepsilon_2}{\gamma_{21}}$.

If $c_1 \varepsilon_2 > c_2 \varepsilon_1$, then $\max I(\tilde{N}_1)$ is attained when $\max \tilde{N}_1 = \frac{\varepsilon_2}{\gamma_{12}}$. It is equal to

$$I_1^* = \frac{c_1 \varepsilon_2}{\gamma_{12}}.$$

Since on OA $\frac{e_2}{\gamma_{12}} = \frac{e_1}{\gamma_{11}}$, $I_1^* = \frac{c_1 e_1}{\gamma_{11}}$.

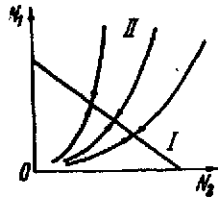


Fig. 27

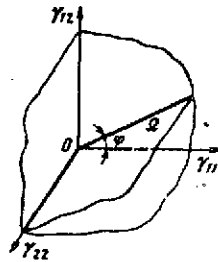


Fig. 28

Fig. 27. Phase portrait of system (62)

Explanation in text

Fig. 28. Feasible region Ω for the two components "predator-prey" system

Thus the optimal value of I on OA coincides with the value of I on one of the planes, which intersect the line OA .

The values of I increase (hyperbolically) as the point under consideration approaches either the edge $0\gamma_{11}$ or the edge $0\gamma_{22}$. In the process either the number of the first species or the number of the second species increases. To which edge is it "more advantageous to move? If the first species is more "valuable" ($I_{\gamma_{11}} < I_{\gamma_{22}}$)

then we should move to the edge $0\gamma_{22}$, if the second species is more "valuable" ($I_{\gamma_{11}} > I_{\gamma_{22}}$) we should move to the edge $0\gamma_{11}$.

In either case the optimal policy is a reduction in the inter-specific competition coefficient $\gamma_{12} = \gamma_{21}$ and an increase in the size of the more "valuable" species which is obtained by decreasing the corresponding intraspecific competition coefficient.

Let us return to the BGC of the "predator-prey" type ($e_2 < 0$, $\gamma_{21} < 0$). We will determine the feasible region Ω . It will lie in the positive octant, and it will contain all points which lie above the plane $e_1\gamma_{12} = -e_2\gamma_{11}$. This region is plotted in Fig. 28.

We have shown above that no point exists in the region Ω at which I takes on a maximum value. Consequently, the maximum value of I is attained on the boundary Ω , and the point $(\gamma_{11}^*, \gamma_{12}^*, \gamma_{22}^*)$ which interests us lies in a small neighborhood of the boundary point. Therefore, as in the first case, we will include in the feasible region also the boundary of Ω (excluding only those points where $I \rightarrow \infty$, in the given case the $0\gamma_{22}$ axis).

We will calculate the values of I on the planes by which Ω is bounded. On the plane $\gamma_{11} = 0$:

$$I_1 = \frac{c_1 \varepsilon_1 \gamma_{22}}{\gamma_{12}^2} + \frac{c_2 \varepsilon_1}{\gamma_{12}} - \frac{c_1 \varepsilon_2}{\gamma_{13}}. \quad (65)$$

On the plane $\gamma_{22} = 0$:

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$$I_2 = \frac{c_2 \varepsilon_2 \gamma_{11}}{\gamma_{12}^2} + \frac{c_2 \varepsilon_1}{\gamma_{12}} - \frac{c_1 \varepsilon_2}{\gamma_{13}}. \quad (66)$$

On the plane $\varepsilon_1 \gamma_{12} + \varepsilon_2 \gamma_{11} = 0$:

$$I_3 = - \frac{c_1 \varepsilon_2}{\gamma_{13}}. \quad (67)$$

Since $\varepsilon_2 < 0$, it follows from a comparison of I_1 , I_2 and I_3 that

$$I_1 \geq I_2, \quad I_1 \geq I_3.$$

By examining (65), we see that I takes on the maximum value for the smallest possible $\gamma_{12} = -\gamma_{21}$ and the largest possible γ_{22} .

In either case the optimal policy is the greatest possible increase in the number of "prey" obtained both from reducing their intraspecific competition coefficient, and from reducing the relative number of "predators," which takes place when γ_{22} is increased and γ_{12} is decreased. The quantity γ_{22} characterizes the intraspecific competition among the "predators" and γ_{12} the "hunter capacity" of the "predator" and the nutrient value of the "prey."

The result is rather paradoxical, but it is easily explained if we recall the type of feedback which relates the number of "predators" and "prey." In practice we never reach the boundary points of Ω , although we may be close. A certain non-zero number of "predators" corresponds to this. By applying our optimal policy and by increasing the number of "prey" we also increase the number of "predators." The result is a rather peculiar conflict situation, since in order to increase the number of "prey" we must decrease the number of "predators," and on the other hand the growth in the number of "prey" is necessarily accompanied by a growth in the number of "predators."

It is clear from these examples that by applying the optimal policy to the formation of a BGC with an optimal trophic structure which has maximum "value" brings us to the boundary of the

stability region. The "most valuable" BGC from our point of view is at the same time also the most unstable BGC. We do not think that nature when it creates existing BGC uses the criterion of their "maximum value"; rather conversely, natural BGC are the most stable systems, but consequently also objects which are extremely difficult to control.

7. Optimal Values of the Competitive Ability Coefficients

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Is it possible to obtain any general results for the optimal values of the coefficients γ_{ij} ? It turns out that it is. Let us assume that in the matrix Γ there is a j -th column (row) such that

$$\det \Gamma = \sum_{i=1}^n \gamma_{ij} M_{ij} \neq 0,$$

where M_{ij} is the cofactor of the element γ_{ij} , and where for at least one pair (k, l) $\gamma_{kl} \neq 0$, $M_{kl} \neq 0$. This is possible, since we assume that system (32) has a unique solution.

Since

$$I = \sum_{i=1}^n c_i \tilde{N}_i = \frac{\sum_{i=1}^n \sum_{j=1}^n c_i M_{ij} e_j}{\sum_{i=1}^n \gamma_{ij} M_{ij}}; \quad (68)$$

and $c_i \neq 0$, when $\det \Gamma \rightarrow 0$ and $M_{ij} \neq 0$, $I \rightarrow \infty$. A necessary and sufficient condition that $\det \Gamma \rightarrow 0$ is that those γ_{kl} tend to zero for which $M_{kl} \neq 0$ ($k = 1, 2, \dots, n$). If by selecting the γ_{ij} the value of the determinant can be made arbitrarily close to zero, then the criterion function I can assume values which are arbitrarily large. In other words one possible optimal policy consists of the following:

1) Either we select one most "valuable" species and we decrease for it as much as possible both the intraspecific competition and the competitive pressure on it by other species (the elements of the row of the matrix Γ which corresponds to the species number must be made as small as possible in absolute value).

2) Or for some selected species we must try to reduce as much as possible competition within the species and the competitive pressure of this species on other species, i.e., to isolate the species from one another as much as possible (this corresponds to a decrease in the absolute value of the elements of the column which was selected in Γ).

It cannot be said that this is the only possible policy; it is very probable that also other policies exist. For this it is necessary that such γ_{ij} exist for which Γ is near-singular, i.e., $\det \Gamma = \mu$, where $\mu > 0$ is a small number.

The result which we obtained can also be interpreted as follows: the optimal policy in either case is the creation of conditions under which the competition within the species is reduced to a minimum, and the species are isolated from one another as much as possible, i.e., we create a structure for which the overlap of the ecological niches is minimal. Under certain conditions such a structure will have little stability. It is very tempting to formulate the following proposition: the most valuable (in the sense of our definition) structures are the least stable structures. However, this statement cannot be applied universally, opposite situations can also exist. The following two sections are devoted to some extent to a study of these problems. /83

8. Stability and the Maximum Utility Criterion

We will show in this paragraph on the example of two competing species how the stability of the BGC and its maximum value are related.

The simplicity of the formulation allows us to demonstrate its solution very clearly on geometric examples.

Suppose that we are given a BGC, consisting of two species which compete for the same food (52). We assume that the coefficients γ_{11} , γ_{12} , γ_{21} , γ_{22} are already given. In the plane $\{N_1, N_2\}$ we will consider the family of lines

$$\begin{aligned} \text{I} \quad N_2 &= \frac{e_1}{\gamma_{12}} - \frac{\gamma_{11}}{\gamma_{12}} N_1 \\ \text{II} \quad N_2 &= \frac{e_2}{\gamma_{22}} - \frac{\gamma_{21}}{\gamma_{22}} N_1 \\ \text{III} \quad N_2 &= \frac{I}{c_2} - \frac{c_1}{c_2} N_1. \end{aligned} \tag{69}$$

Let $\varepsilon_1 \gamma_{21} < \varepsilon_2 \gamma_{11}$; $\varepsilon_2 \gamma_{12} < \varepsilon_1 \gamma_{22}$. Then the point A in Fig. 29, a, b is stable, and the points B and C are not stable. Ignoring for the moment stability and instability, we will see at which of them the criterion function $I = c_1 \tilde{N}_1 + c_2 \tilde{N}_2$ is a maximum. Geometrically this is equivalent to selecting from among the three lines from the family III which pass through these points one line, such that the segment which it cuts off on the ON_2 axis is as large as possible, i.e., the quantity I/c_2 is a maximum and consequently also the quantity I is a maximum (when c_2 is fixed). It is easily seen that if

$$\frac{\gamma_{11}}{\gamma_{12}} > \frac{c_1}{c_2} > \frac{\gamma_{21}}{\gamma_{22}}, \quad (70)$$

the unknown line passes through the point A, and $\max I = I_A$ (see Fig. 29, a). If

$$\frac{c_1}{c_2} < \frac{\gamma_{21}}{\gamma_{22}}, \quad (71)$$

we must select the line which passes through the point B and $\max I = I_B$ (see Fig. 29, b). Finally, if

$$\frac{c_1}{c_2} > \frac{\gamma_{11}}{\gamma_{12}}, \quad (72)$$

$\max I = I_C$.

Thus, until condition (70), is satisfied, the requirements that /84 the BGC be stable and that it have maximum value do not contradict one another. When (70) is not satisfied (either (71) or (72) holds) the maximum of the criterion function is attained for an unstable solution, and the requirements of stability and maximum value contradict one another.

How will the graphs change in Fig. 29, a when the parameters γ_{ij} are varied? If we decrease the quantities γ_{12} and γ_{21} which describe the interspecific competition, the point A which remains as before stable, will move farther away from the coordinate origin. In the process I_A will also increase (Fig. 30). But it will not increase without limit: the maximum value is

$$I_A = I_{A_0} = \frac{c_1 \varepsilon_1}{\gamma_{11}} + \frac{c_2 \varepsilon_2}{\gamma_{22}}$$

(see Section 6). It is attained when $\gamma_{12} = \gamma_{21} = 0$, i.e., when the ecological niches of these two species do not overlap. We note that in this limiting case inequality (70) is satisfied for any strictly positive c_1 and c_2 .

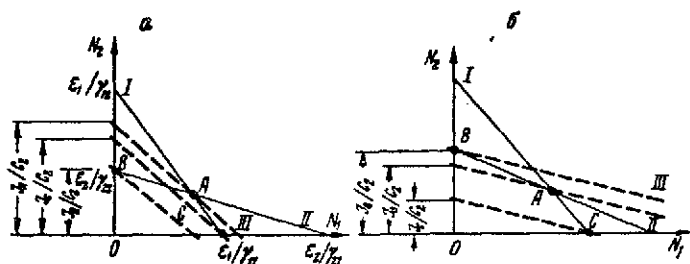


Fig. 29. Stable state of a system consisting of two competing species and the values of the criterion function for various relations between the coefficients γ_{ij} and the costs c_1

and c_2

a-- $\gamma_{11}/\gamma_{12} > c_1/c_2 > \gamma_{21}/\gamma_{22}$, b-- $c_1/c_2 < \gamma_{21}/\gamma_{22}$, A-stable

stationary point, B,C-unstable stationary points

The criterion function increases also when the quantities γ_{11} and γ_{22} decrease (Fig. 31). But sooner or later $c_1\gamma_{21} > c_2\gamma_{11}$ or $c_1\gamma_{22} < c_2\gamma_{12}$ or both of these inequalities will be satisfied simultaneously. We will consider the latter case. Here the points B" and C" will be stable and the point A" will be unstable. This corresponds to one of the species dying out, and consequently to degeneration of the BGC. Characteristically because of the concavity of OB"A"C", the maximum of I will be attained at B" or at C" and never at A", so that when the BGC is degenerate, the maximum is attained only on stable solutions. If $c_1\gamma_{11} > c_2\gamma_{22}$, then $\max I = I_0''$, if $c_1\gamma_{11} < c_2\gamma_{22}$, then $\max I = I_c''$ (see section 6). A further decrease in γ_{11} or γ_{22} leads to an unbounded increase in the criterion function I.

Generalizing everything that was said above, we reach conclusions which are analogous to those made in Section 6. In either case the optimal policy consists of reducing the interspecific and intraspecific competition coefficients. If a reduced interspecific interaction and greater isolation of ecological niches does not reduce the stability of the BGC (or in a certain sense even increases it, leading to the result that for any cost ratios a non-degenerate BGC with a stable non-zero state for both species is most valuable), the reduced intraspecific competition even though

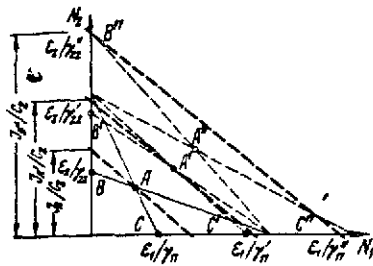


Fig. 30

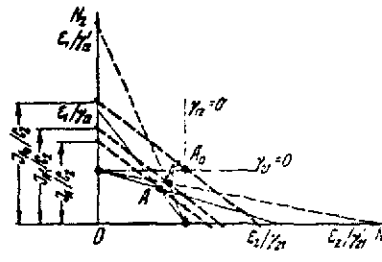


Fig. 31

Fig. 30. Change in the position of the stable point and the value of the criterion function as the intraspecific competition coefficient decreases

Fig. 31. Change in the position of the stable point, stability loss, and the change in the criterion function as the inter-specific competition coefficient decreases

it leads to a greater value of the BGC, leads at the same time, to a loss of stability of the BGC and to its degeneracy. The optimal policy is to leave only one species, but this contradicts the "non-deterioration" policy of the BGC as a whole. The simultaneous application of two such types of decisions makes it possible to use both species, i.e., preserve the BGC, but as shown in Section 6, this brings the system sufficiently close to the stability boundary.

9. Maximally Stable Biosystems

Situations may occur in which we are not interested in the value of the BGC, but what is necessary is maximum stability of the entire system. When such requirements are made, it is assumed implicitly, that the concept of a "maximally stable BGC" is intuitively clear, and requires no further study. However, this is not the case at all. Even in stability theory and in applied disciplines related to it in one way or another a variety of different definitions of stability exist (Letov, 1962). Therefore, the selection of the stability criterion for a system such as a BGC is a very difficult problem. We will demonstrate on a sufficiently simple example of two competing species several possible stability criteria for such a system and we will show how they are interrelated. The form of these criteria will be demonstrated by the type of disturbances acting on the system. /86

1. Suppose that the BGC consisting of two species competing for the same food is described by the system (52). The main type of disturbances acting on the BGC will be the perturbations in the parameters γ_{11} , γ_{12} , γ_{21} , γ_{22} . It is clear that when the perturbations are sufficiently large, the system may leave the stability

CS

region, and one of the species will perish. We will assume that the perturbations in all parameters are equally probable. When $\gamma_{12} = \gamma_{21}$ the stability region coincides with the feasible region Ω plotted in Fig. 26. The farther the point whose parameters are selected for the unknowns lies from the planes $\epsilon_1 \gamma_{22} - \epsilon_2 \gamma_{11} = 0$, $\epsilon_2 \gamma_{11} - \epsilon_1 \gamma_{21} = 0$, the smaller the probability that the perturbations of the parameters will make the system unstable. We assume here implicitly that the probability of the perturbation is inversely proportional to its magnitude. But there is a constraint given by the species in the BGC itself: $\gamma_{12} \geq 0$. Consequently, the locus of the points which are farthest from the planes and which satisfy this constraint must lie on the plane $\gamma_{12} = 0$. Without dwelling on details we will see immediately that the locus sought may be a line on which the centers of all halfspheres inscribed in the trihedral angle lie (Fig. 32). The coordinates of the center of the halfsphere of the largest possible radius are the parameters sought. If the quantity γ_{12} is bounded below, so that $\gamma_{12} \geq \mu > 0$, then the centers of the halfspheres must lie in the plane $\gamma_{12} = \mu$.

Thus, when the parameters are perturbed, which is equivalent to disturbances of the environment, a system in which the species are most isolated from one another is the most stable system. Clearly this is a natural result for two species which compete for food. If the species are related by relations of the "predator-prey" type, it can be shown that an increase in the isolation of the species leads to decreased stability.

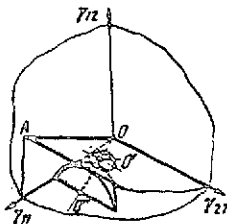


Fig. 32. Halfspheres inscribed in trihedral angle in the feasible region Ω .

O' , O'' centers of these halfspheres

We will construct the phase portrait for a system consisting of two coexisting species (Fig. 33, a, b). The inequalities which determine the stability are related to the length of the BD and CF segments. It is clear that the longer the segments, the less probable a situation in which $OB > OD$ or $OC > OF$, or both inequalities are satisfied simultaneously.

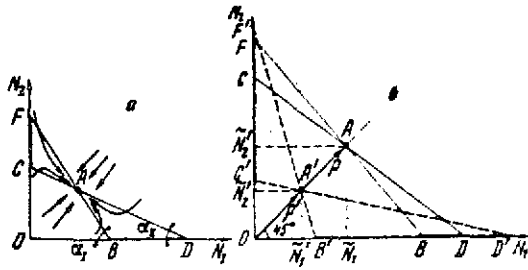


Fig. 33. Various stability criteria:

a--phase portrait of a system consisting of two competing species.

The length of the segments BD and CF , and also the difference between the angles α_I and α_{II}

characterize the stability of the system; b--stability criterion, the quantity $\rho=OA$. However, if for a corresponding change in the coefficients γ_{ij} BD in-

creases to $B'D'$, and CF to $C'F'$, ρ decreases to $\rho = OA'$. Thus, an increase in the stability by one criterion can be accompanied by a decrease by the other.

Therefore, these requirements must somehow be reflected in the stability criterion by the parameters. The form of the criterion is determined to a large extent by the metric we use. We will give a number of possible criteria. We assume that the stability conditions $\varepsilon_2 \gamma_{11} > \varepsilon_1 \gamma_{21}$, $\varepsilon_1 \gamma_{22} > \varepsilon_2 \gamma_{12}$ are satisfied:

a) The parameters of the system which take into account all constraints must be selected in such a way that the quantity

$$S = \sqrt{(BD)^2 + (CF)^2} = \sqrt{\left(\frac{\varepsilon_2}{\gamma_{21}} - \frac{\varepsilon_1}{\gamma_{11}}\right)^2 + \left(\frac{\varepsilon_1}{\gamma_{12}} - \frac{\varepsilon_2}{\gamma_{22}}\right)^2}; \quad (73)$$

is a maximum.

b) The parameters of the system must be selected in such a way that

$$\max_{\gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22} \in \Omega} \min \{BD, CF\} = \max_{\gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22} \in \Omega} \min \left\{ \left(\frac{\varepsilon_2}{\gamma_{21}} - \frac{\varepsilon_1}{\gamma_{11}} \right); \left(\frac{\varepsilon_1}{\gamma_{12}} - \frac{\varepsilon_2}{\gamma_{22}} \right) \right\}, \quad (74)$$

where Ω is some feasible region.

c) We introduce the following notation:

$$\alpha_I = \arctg \frac{\gamma_{11}}{\gamma_{12}}; \quad \alpha_{II} = \arctg \frac{\gamma_{21}}{\gamma_{22}}; \quad \alpha_I, \alpha_{II} \in \left[0, \frac{\pi}{2} \right].$$

Then still another stability criterion can be defined as

$$\max_{\gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22} \in \Omega} \{\alpha_1 - \alpha_{11}\}. \quad (75)$$

2. Suppose that the BGC is in the stationary state $(\tilde{N}_1, \tilde{N}_2)$, where

$$\tilde{N}_1 = \frac{e_1 \gamma_{22} - e_2 \gamma_{12}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}; \quad \tilde{N}_2 = \frac{e_2 \gamma_{11} - e_1 \gamma_{21}}{\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21}}. \quad (76)$$

Suppose that the disturbances are such that as a result of their action the equilibrium stationary sizes change instantaneously, where the number of one or both species can be zero after which the BGC can no longer leave this state (the state is not recurrent). In Fig. 33, a this means that the point A can either be on the ON_1 axis or on ON_2 . If the deviations both from N_1 and from N_2 are equally probable, the requirement for maximum stability for such type of perturbations reduces to the following: the point A must be as far as possible from ON_1 , and from ON_2 , and the stability conditions must be not be violated. The equiprobable assumption implies that point A must lie on the line which passes through the coordinate origin at a 45° angle, i.e.,

$$\left. \begin{aligned} e_1 (\gamma_{21} + \gamma_{22}) &= e_2 (\gamma_{11} + \gamma_{12}) \\ \rho &= \sqrt{(\tilde{N}_1)^2 + (\tilde{N}_2)^2} = \tilde{N}_1 \sqrt{2} = \tilde{N}_2 \sqrt{2} \end{aligned} \right\} \quad (77)$$

is a maximum (see Fig. 33, b). If we also require that at least the stability margin in the parameters which is determined in accordance with one of the criteria introduced above be not reduced, the process of selecting the most stable BGC reduces to finding the smallest possible γ_{12} and γ_{21} . As a result of this operation ρ increases and the stability of the system to perturbations in the stationary size levels increases. As in case 1, the most stable system is a system in which the species are most isolated from one another. On the other hand an increase in ρ due to a decrease in the coefficients γ_{11} and γ_{22} can lead to loss of stability in the parameters and to a degenerate BGC. It can be said that the criteria which were formulated for the two types of perturbations under consideration are contradictory to some extent.

3. Finally we will formulate a third type of criterion which will be based on the requirement that the perturbations

be "corrected" in minimum time. Such criteria are widely used in automatic control theory. If we denote by $\delta N_i = N_i - \tilde{N}_i$, $i = 1, 2$, the deviations from the stationary state, then

$$\delta N_i = \delta N_{i0} e^{\lambda_i t},$$

where the λ_i are the eigenvalues of the matrix

$$\left\| \frac{\partial f_i}{\partial N_j} \right\|_{\tilde{N}_i} = \| -\gamma_{ij} \tilde{N}_i \|; \quad i, j = 1, 2.$$

If the stability conditions are satisfied, $\lambda_i < 0$ (in a system consisting of two competing species, the λ_i are real). The converse proposition is also valid. It is clear that the larger the absolute value of λ_i , the faster the perturbations are "corrected" and the faster $\delta N_i \rightarrow 0$. The character of the con-

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vergence can be defined in various ways: either this is the fastest convergence to zero of all mean deviations, or it is the fastest convergence of the coordinate which is "corrected" most slowly, etc. Various definitions lead to various ways of introducing the metric and the norm, and as a result to various forms in which the maximum stability criterion can be written.

For example, we can require

$$\max_{\gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22} \in \Omega} \min \{ |\lambda_1|; |\lambda_2| \}. \quad (78)$$

This criterion ensures the fastest decrease in the perturbation which decreases most slowly. What does it lead to in the case of two competing species? We will calculate the eigenvalues:

$$\lambda_{1,2} = \frac{1}{2} \{ -(\gamma_{11} \tilde{N}_1 + \gamma_{22} \tilde{N}_2) \mp \sqrt{(\gamma_{11} \tilde{N}_1 - \gamma_{22} \tilde{N}_2)^2 + 4\gamma_{12}\gamma_{21}\tilde{N}_1\tilde{N}_2} \}. \quad (79)$$

It follows from (78) and (79) that when we set up a system which corrects most quickly the perturbations we must find

$$\max_{\gamma_{11}, \gamma_{12}, \gamma_{21}, \gamma_{22} \in \Omega} \{ \gamma_{11} \tilde{N}_1 + \gamma_{22} \tilde{N}_2 - \sqrt{(\gamma_{11} \tilde{N}_1 - \gamma_{22} \tilde{N}_2)^2 + 4\gamma_{12}\gamma_{21}\tilde{N}_1\tilde{N}_2} \};$$

where \tilde{N}_1, \tilde{N}_2 are determined from formula (76). It is easily seen

that the expression to be maximized over the γ_{ij} under the maximum symbol increases when the coefficients γ_{ij} decrease. In addition to this it can be shown that when $\det \Gamma = \gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21} \rightarrow 0$, it takes on arbitrarily large values. Consequently the maximum stability requirement in accordance with this criterion and maximum stability in the parameters are contradictory, so that a typical conflict situation arises. We note that in the given case the policy of selecting the coefficients in accordance with such maximum stability criterion and the maximum cost criterion coincide.

The reader probably noted already the cursory and somewhat disconnected presentation in this chapter. Many interesting problems which deal directly with this theme were not touched on. Often, for the sake of clarity, we sacrificed generality and rigor of the presentation. To some extent this was justified by the fact that in the quest for generality we would have to increase considerably the bulk of this chapter. A whole host of problems which are close in the manner in which the decisions are made cannot be solved by the methods given here. Their presentation would violate the unity of the chapter. For example, V. S. Ten solved the very interesting problem of the "predator"-polyphage feeding conditions. But the methods which he uses are methods of queuing theory and they are not along the general lines of our book. Therefore, we will not present this problem.

When we discussed the general formulations of the problems we deliberately did not make them concrete, the same can also be said about simplified problem models. If we so desire we can "apply" these models to concrete situations by selecting the appropriate coefficients.

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In conclusion we shall dwell on the biological aspects of these problems, on the possibility of making such type of decision. We note that the results which we obtained, despite their somewhat unusual formulation, have been known and used widely in practice for a long time. In fact, the usual type of agrocoenosis is a monoculture which is isolated in various ways from the species which act on it. If several species are used in agrocoenosis, they are related to one another either by relations of the "predator-prey" type, by symbiotic relations, or their ecological niches are sufficiently isolated from one another.

The best way of acting on the BGC is by changing the external environment, both its abiotic and biotic parts. In fact, this determines the change in the quantities which characterize this environment, the competitive ability coefficients. How can it be changed? For the time being, evidently by changing the BGC structure, which is determined both by the structural diagram, the graph, and by the effectiveness with which the arcs of the trophic chains operate. The magnitudes of the flows on the given structures.

The effectiveness of the operation is determined by the specific characteristics of the dominant species and the character of the interrelations among them. These characteristics depend not only on the general parameters of the environment (climate, geomorphology, etc.), but also on the specific parameters of a concrete biotope (the structure of the soil, its chemical composition, etc.), which can already be regulated given the contemporary level of agrobiotechnology.

The most real form of control under contemporary conditions is regulating the number of existing species, and acclimatization of new species, i.e., changing the BGC structure. Actions of this type are also used rather widely now, however, without taking into account the consequences of their application. When we formulated the problem, we already attempted to study the entire BGC system as a whole, taking into account the interrelations among all species making up the BGC. We note that taking into account the interrelations among all species is not equivalent at all to a full description. Only the dominant species, or species which are important in some other respect, are isolated and described more or less completely, all remaining species are averaged in some sensible way, and the model includes only these averaged parameters.

CHAP. VI. OPTIMIZATION PROBLEMS WHICH TAKE INTO ACCOUNT THE AGE STRUCTURE, VARIOUS SIZES OF THE INDIVIDUALS AND OTHER FACTORS

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1. Taking Into Account the Age Structure in Biogeocoenosis Models

Until now we used for the phase variables when we described the BGC the values of the numbers (biomasses) of the species in it. We naturally assumed complete homogeneity of the individuals within the population of one species. The same quantities were also included in the solution of optimization problems.

But when we formulate optimization problems of a certain type, (for example, when only individuals of a certain age are caught, or when individuals of various sizes are valued in different ways, etc.), it is necessary to take into account the character of the distribution of individuals of one species by certain characteristics, age, size, etc.

Suppose that the populations of various species which make up the BGC consist of individuals of different ages. What will be the model of such a system?

The most general model (46) which was given in Section 1 of the preceding chapter made allowance for various age groups in the populations of various species. Each age group was characterized

by its number and was in fact considered as a separate species with its own competitive ability coefficients. This model was discrete-continuous, since the sizes of discrete age groups vary continuously in time.

As an example of a discrete-continuous model we considered a BGC of the "predator-prey" type in which the "predators" feed only on adult "prey" individuals. If N_1 is the number of young "prey," N_2 is the number of adult sexually mature "prey" individuals and N_3 is the number of "predators," then following Kostitzin we can write

$$\left. \begin{aligned} \frac{dN_1}{dt} &= e_1 N_2 - (\alpha + m) N_1 \\ \frac{dN_2}{dt} &= -m N_2 + \alpha N_1 - \gamma_{23} N_2 N_3 \\ \frac{dN_3}{dt} &= -e_3 N_3 + \gamma_{32} N_2 N_3 \end{aligned} \right\}. \quad (80)$$

Here e_1 is the growth coefficient of the "prey," m is their natural mortality coefficient, α is a quantity which characterizes the probability that a young "prey" individual will reach the age of sexual maturity, e_3 is the mortality coefficient for the "predator," γ_{23} , γ_{32} are coefficients which characterize the competitive relations among the "predators" and "prey." /92

System (80) has the stationary point

$$\tilde{N}_1 = \frac{e_1 e_3}{(\alpha + m) \gamma_{32}}; \quad \tilde{N}_2 = \frac{e_3}{\gamma_{32}}; \quad \tilde{N}_3 = \frac{\alpha e_1 - m(\alpha + m)}{(\alpha + m) \gamma_{23}}.$$

If the "prey" is highly fertile (e_1 is large) and its young individuals are sufficiently viable, so that the inequality $\alpha e_1 > m(m + \alpha)$, is satisfied, the state characterized by the point $(\tilde{N}_1, \tilde{N}_2, \tilde{N}_3)$ is stable. If the mortality of the "predators" is sufficiently high, so that

$$e_3 > \frac{(m + \alpha) [\alpha e_1 - m(m + \alpha)]}{\alpha^2 e_1^2},$$

the stationary state (80) is a focus, and the number of "predators" and "prey" perform damped oscillations about this point. If the

mortality of the "prey" is high, so that

$$\alpha e_1 < m(m + \alpha),$$

both species die out.

It is easily seen that the problem of collecting the yield in system (80) is solved in exactly the same way as in a system consisting of three different species which are not divided into age groups. But the difficulties connected with the solution of the problem increase sharply if a large number of age groups must be taken into account since the dimensionality of the problem increases.

A natural generalization of the discrete-continuous model is a model in which both time and age are considered as continuous variables (continuous model). We will give an example of such a model (Foerster, 1959; Ginzburg, 1968). Suppose that a population of some species exists in an environment with constant external conditions. By $N(x, t)$ we will denote the number of individuals whose age, at the instant t , is equal to x . Then the number of individuals of all ages is defined as

$$\bar{N}(t) = \int_0^{\infty} N(x, t) dx$$

(when we integrate we also take into account individuals whose age is "infinite," but this is merely a formality which has no effect on the results). Thus, $N(x, t)$ can be considered as the population "age density." We will introduce the following notation: $n(x)$ is the natality coefficient for individuals of age x , $m(x)$ is the natural mortality coefficient for individuals of age x , $\gamma(x, y)$ is a coefficient which characterizes the competition between individuals of ages x and y .

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Without dwelling on details of the derivation we write the equation for the age density:

$$\begin{aligned} \frac{\partial N}{\partial t} + \frac{\partial N}{\partial x} &= - \left[m(x) + \int_0^{\infty} \gamma(x, y) N(y, t) dy \right] N; \\ N(0, t) &= \int_0^{\infty} n(x) N(x, t) dx; \\ N(x, 0) &= g(x). \end{aligned} \tag{81}$$

Integrating (81) with respect to x and using the mean value theorem, we obtain:

$$\frac{d\bar{N}}{dt} = \bar{N} [n(\xi_1) - m(\xi_2) - \gamma(\xi_3, \eta_1) \bar{N}]. \quad (82)$$

Here $n(\xi_1)$, $m(\xi_2)$ are values which were taken at some point $x \in [0, \infty)$, $\gamma(\xi_3, \eta_1)$ are values which were taken at some point of the region:

$$x \in [0, \infty); y \in [0, \infty); \bar{N}_0 = \int_0^\infty g(x) dx.$$

Equation (82) is a typical logistic equation, since the entire population size changes in accordance with the logistic law.

2. Stationary Collection of the Yield in a Population Consisting of Two Age Groups

Suppose we are given a BGC consisting of the population and the surrounding environment. All individuals in the population are divided into two age groups: young individuals who did not reach sexual maturity (N_1) and adult (N_2) mature individuals. We will assume that there is no competition among the adult and young individuals, and that there is no competition within the young group, a situation which is characteristic of large mammals (for example, among insects the situation is reversed: maximum competitive struggle occurs in the larva stage). Under these assumptions the model of such a system can be written in the form

$$\left. \begin{aligned} \frac{dN_1}{dt} &= e_1 N_2 - (\alpha + m_1) N_1 \\ \frac{dN_2}{dt} &= -m_2 N_2 + \alpha N_1 - \gamma_{22} N_2 \end{aligned} \right\}. \quad (83)$$

Here e_1 is the natality coefficient, m_1 and m_2 are the natural mortality coefficients of the young and adult individuals, α is a coefficient which characterizes the probability that the young individuals will reach sexual maturity. This system has the stationary point

$$\left. \begin{aligned} \tilde{N}_1 &= \frac{e_1 [e_1 \alpha - m_2 (\alpha + m_1)]}{\gamma_{22} (\alpha + m_1)^2} \\ \tilde{N}_2 &= \frac{e_1 \alpha - m_2 (\alpha + m_1)}{\gamma_{22} (\alpha + m_1)} \end{aligned} \right\}. \quad (84)$$

The point $(\tilde{N}_1, \tilde{N}_2)$ is stable if $\epsilon_1 \alpha > m_2(\alpha + m_1)$ (stable node). Figure 34 shows the phase portrait of system (83).

$$\begin{array}{ll} \text{I} & N_1 = \frac{\epsilon_1}{\alpha + m_1} \cdot N_2, \\ \text{II} & N_1 = \frac{\gamma_{22}}{\alpha} N_2^2 + \frac{m_2}{\alpha} N_2. \end{array}$$

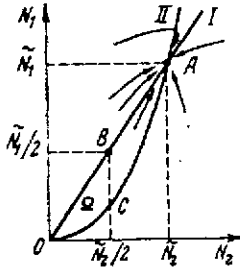


Fig. 34. Phase portrait of system (83)
Explanations in text.

It is easily seen that when the propagation rate is sufficiently fast and the infant mortality is low and when the probability of reaching the reproductive age is sufficiently large, the point $A(\tilde{N}_1, \tilde{N}_2)$ will always lie in the positive quadrant and it will be stable.

As in Chapter IV, we will here formulate the problem of the stationary collection of the yield with the additional "nondeterioration" conditions for the BGC. The yield collection step is considered to be sufficiently small. In other words we must determine

$$I^* = \max_{N \in \Omega} I,$$

where

$$I = c_1 [\epsilon_1 N_2 - (\alpha + m_1) N_1] + c_2 (\alpha N_1 - m_2 N_2 - \gamma_{22} N_2^2) \quad (85)$$

in the region

$$(\Omega) \begin{cases} \epsilon_1 N_2 - (\alpha + m_1) N_1 \geq 0 \\ \alpha N_1 - m_2 N_2 - \gamma_{22} N_2^2 \geq 0. \end{cases} \quad (86)$$

Thus, since N_1 enters I linearly, the maximum value must be reached on the boundary of Ω on the line

$$\begin{aligned} N_1 &= \frac{s_1}{\alpha + m_1} \cdot N_2, \\ I_I &= \frac{c_2 N_2}{\alpha + m_1} \cdot [\alpha e_1 - m_2 (\alpha + m_1) - \gamma_{22} (\alpha + m_1) N_2]. \end{aligned} \quad (87)$$

The maximum of (87) on N_2 is attained at the point

$$N_2^* = \frac{\alpha e_1 - m_2 (\alpha + m_1)}{2\gamma_{22} (\alpha + m_1)} = \frac{1}{2} \tilde{N}_2$$

and it is equal to

$$I_I^* = \frac{c_2 [\alpha e_1 - m_2 (\alpha + m_1)]^2}{4\gamma_{22} (\alpha + m_1)^2}. \quad (88)$$

On the parabola

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$$N_1 = \frac{\gamma_{22}}{\alpha} N_2^2 + \frac{m_2}{\alpha} N_2,$$

$$I_{II} = \frac{c_1 N_2}{\alpha} [\alpha e_1 - m_2 (\alpha + m_1) - \gamma_{22} (\alpha + m_1) N_2]. \quad (89)$$

The maximum of (89) on N_2 is attained at the same point $N_2^* = \frac{1}{2} \tilde{N}_2$ at which

$$I_{II} = \frac{c_1 [\alpha e_1 - m_2 (\alpha + m_1)]^2}{4\gamma_{22} (\alpha + m_1) \cdot \alpha}. \quad (90)$$

Comparing (88) and (90), we see that when

$$\alpha c_2 > c_1 (\alpha + m_1), \quad (91)$$

I takes on the maximum at the point B (see Fig. 34) with the coordinates

$$N_{1B} = \frac{\tilde{N}_1}{2}; \quad N_{2B} = \frac{\tilde{N}_2}{2}, \quad (92)$$

and when

$$ac_2 < c_1(a + m_1) -$$

at the point C with the coordinates

$$N_{1C} = \frac{r_2(x + m_1)^2}{4\alpha s_1^2} \cdot \tilde{N}_1^2 + \frac{m_2(x + m_1)}{2\alpha s_1} \tilde{N}_1; \quad N_{2C} = \frac{\tilde{N}_2}{2}.$$

If the ratio of the costs is such that inequality (91) holds, the optimal yield collection process consists of the following: the sizes of both age groups are held on the constant levels which are determined by the coordinates of the point B, and the yield which is collected is the increment in the number of adult individuals. Since the point B is not a stationary point of the system, the number of adult individuals increases in the time which is equal to one step of the process (the number of young individuals remains unchanged). This increment is collected as the yield.

If inequality (92) holds, the optimal process is the process for which the sizes of both groups are held on the constant levels determined by the coordinates of the point C, and only the increment in the young individuals is collected.

Such an alternative character of the decision is obviously connected with the selection of a model which is linear in N_1 .

If we assume that also within the young group competition exists, then we can hope that an optimal point (N_1^*, N_2^*) which lies within the feasible region exists. In this case we will collect as the yield the increment in the number of both age groups.

3. Optimal Age Distributions. Possible Formulations of the Problems.

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When the age factor is taken into account, the state of the population is described not by one number, the population size at a given instant of time, but by the entire distribution, which also varies over time. The selection of the age distribution can be one of the decision parameters. In addition to this also other decisions lead to the formation of a definite age distribution, which we will call optimal if the decision made is optimal.

We will give a small example related to the optimal catch problem. Suppose that we are given a certain ichthyocoenosis. If the individuals of the coenosis are not caught, then a stationary age distribution is formed in it. As soon as fishing

begins, this distribution changes: if the same fishing policy is used long enough, the new distribution can also become stationary. Naturally to each policy will correspond its own distribution. The optimality criterion is usually related to the differences among the new and old types of distributions, for example, the maximum biomass criterion for the biomass caught for forming and maintaining the new distribution. To the maximum of this criterion corresponds its own age distribution which will be optimal for the given problem.

What will the problem of optimizing the process of collecting the yield for the system described by equations (81) look like? Analogously as in Chapter II, the time interval $[0, T]$ in which the collection takes place is broken up into n equal parts by the points $t_i = h, 2h, \dots, nh = T$. In each step an amount of biomass of all ages is removed from the population which is equal to

$$\int_0^{\infty} k_i(x) N_i^-(x) dx; \quad i = 1, 2, \dots, n.$$

Here $0 \leq k_i(x) \leq 1$, $i = 1, 2, \dots, n$ are admissible decisions. Then during the transition from one step to another

$$N_{i+1}^+(x) = N_i^-(x) [1 - k_i(x)], \quad (93)$$

where the index $(-)$ denotes the state of the system to the left and the index $(+)$ to the right of t_i . In order to explain how the state of the system changes during the transition from t_i to t_{i+1} (in one step), we must solve equations (81). If we can find a solution then

$$N_i^-(x) = N(t_{i+1}^-, x) = P\{N_i^+(x)\} = P\{N(t_i^+, x)\}. \quad (94)$$

Suppose that we are given the function $c_i(x)$ the cost per unit biomass or per one individual of age x . We assume for simplicity that $c_i(x) \equiv c(x)$ is independent of i . The return in one step of the process is equal to

$$g_i = \int_0^{\infty} c(x) k_i(x) N_i^-(x) dx; \quad i = 1, 2, \dots, n. \quad (95) \quad \underline{/97}$$

The total return is the sum of returns over all n steps. We introduce the return function $f_i[N(x)]$, which is equal to the total

return after i collection steps, assuming that in the preceding steps optimal decisions were made. In the given case the return function is a functional of $N(x)$. Applying Bellman's optimality principle we obtain

$$\left. \begin{aligned} f_1(N) &= \max_{0 \leq k(x) \leq 1} \int_0^{\infty} c(x) k(x) N(x) dx; \\ f_i(N) &= \max_{0 \leq k(x) \leq 1} \left\{ \int_0^{\infty} c(x) k(x) N(x) dx + f_{i-1} \{P[(1-k(x))N(x)]\} \right\}. \end{aligned} \right\} \quad (96)$$

Here $N(x) = N_1^-(x)$ is the age distribution in the population at the instant when collection takes place for the first time.

$P[\dots]$ is the transition operator in one step (94). The solution of this functional equation gives the unknown optimal decisions. Unfortunately, such a problem is very complex. One of the possible approaches to its solution is to replace the continuous distributions by discrete distributions with a small number of points. This is analogous to formulating the optimality problem for models with several age groups. The dimension of the problem will be equal to the number of these groups.

In addition to such an approach to the problem, its solution can be simplified considerably if we assume that the collection process is stationary (in the theory of dynamic programming, said to be infinite, since $n \rightarrow \infty$). In this case we seek the maximum of the function

$$\max_{k \geq 1} \int_0^{\infty} c(x) k_i(x) N_i^-(x) dx.$$

The basic functional equation has the form:

$$\begin{aligned} f[N(x)] &= \max_{0 \leq k \leq 1} \max \left\{ \int_0^{\infty} c(x) N(x) dx, f\{P[(1-k(x))N(x)]\} \right\} = \\ &= \max_{0 \leq k \leq 1} \left\{ \int_0^{\infty} c(x) N(x) dx, \max_{0 \leq k \leq 1} f\{P[(1-k(x))N(x)]\} \right\}. \end{aligned} \quad (97)$$

Even though in this problem we must find one $f(N)$, instead of a sequence of functionals $f_i(N)$, the problem did not become simpler.

We can proceed somewhat differently, and consider the stationary process as a limit determined by equations (96) as $n \rightarrow \infty$,

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and not directly from the form of the return function as we did above. Then:

$$f(N) = \max_{0 \leq k(x) \leq 1} \left\{ \int_0^{\infty} c(x) k(x) N(x) dx + f\{P[(1 - k(x)) N(x)]\} \right\}. \quad (98)$$

If the operator P has a convenient structure, then the method of successive approximations naturally suggests itself for the solution of (98). In many concrete cases determining the convergence of this method will not be apparently a very difficult problem.

The optimum decision $k(x)$ which is found from solving (98) has the property that the initial age distribution altered by its application is again restored at the next collection instant. In the solution all the information about the dynamics of the age composition is used. If the solution of system (81) is unique, then for a fixed step we obtain the unique initial age distribution which ensures that the process is stationary. However, the requirement that the initial distribution be completely restored is too strong. In a real situation it is fully adequate if the total population size or the number of certain age groups do not decrease (for example, the number of newborn individuals). These requirements may be satisfied, but the age distribution itself need not be restored at the next collection, it may vary from step to step so that we cannot speak here about strict stationarity. But on the average the process will be stationary. To find the optimal decision, it suffices if information is available about some average behavior of the system. The new problem will be formulated as follows: in each step of the process we seek a decision $0 \leq k(x) \leq 1$ which will yield the maximum return

$$g(N^-, k) = \int_0^{\infty} c(x) k(x) N^-(x) dx. \quad (99)$$

Here $N^-(x)$ is the initial age distribution to which the decision $k(x)$ is applied. It is clear that these distributions can vary in the current and successive steps, so that also the decision $k[N(x)]$ may be different. In fact we replaced the optimality principle by the local optimality requirement, and in each step we solve an optimality problem which is independent of the preceding step.

Let us consider (99). It is easily seen that for any $N^-(x)$ $\max_{0 \leq k \leq 1} g(N^-, k)$ is attained when $k(x) \equiv 1$, i.e., the collection process terminates in the first step. This is unwise, since it is more convenient to retain a certain part of the population so that it can be reproduced at the instant when the next collection takes place.

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If we retain a certain total number ignoring age, then

$$\int_0^{\infty} N^+(x) dx \geq c_0 \text{ when } \int_0^{\infty} k(x) N^-(x) dx \leq A_0 - c_0; \quad A_0 = \int_0^{\infty} N^-(x) dx. \quad (100)$$

However, solutions can be obtained which will preserve the total number, but which will leave individuals not capable of reproduction (because of age). Evidently another condition is needed which takes into account this fact. Nevertheless, we may still use (100), but with an appropriately selected constant c_0 (we will describe later one of the ways of selecting this constant).

Another condition may be a lower bound on the number of newly born individuals in the population, since when a certain number of these is maintained in the population, it is possible to ensure that also the total population size does not decrease. This condition can be written in the form $N^+(0) \geq c_1$, or using (81) and (93)

$$\int_0^{\infty} k(x) n(x) N^-(x) dx \leq A_1 - c_1; \quad A_1 = \int_0^{\infty} N^-(x) dx. \quad (101)$$

Here $n(x)$ is the natality coefficient.

If the population is in the logarithmic growth phase (the effect of the term with $\gamma(x, y)$ in (81) is small), we can take for the condition a lower bound on the rate of growth, so that

$$\int_0^{\infty} [n(x) - m(x)] N^+(x) dx \geq c_2;$$

or

$$\begin{aligned} \int_0^{\infty} [n(x) - m(x)] k(x) N^-(x) dx &\leq A_2 - c_2; \\ A_2 &= \int_0^{\infty} [n(x) - m(x)] N^-(x) dx. \end{aligned} \quad (102)$$

In all these inequalities the constants $A_i - c_i$, $i = 0, 1, 2$ must be nonnegative. Also other constraints may exist, for example, if certain costs are incurred in the fishing process, it is natural to assume that the total cost in one step must not exceed a

certain level, so that

$$\int_0^{\infty} z(x) k(x) N^-(x) dx \leq c_3. \quad (103)$$

Here $z(x)$ are the costs incurred in catching one individual of age x .

If we now seek the decision maximizing $g(N, k)$ with one or several constraints (100) - (103), we obtain a typical infinite dimensional linear programming problem. One powerful method used for solving such problems is the Neyman-Pearson lemma (Bellman, Glicksberg, Gross, 1962). The optimum decision is a relay function, i.e., a function which is equal to one on some segments of the halfline $0 \leq x < \infty$, and to zero at almost all remaining points.

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It is possible to formulate problems for which the decision $k(x)$ is already given (below we will study this problem in detail) and we must find the initial age distribution which "fits" in the best manner the given decision. Mathematically this problem is completely equivalent to the previous problem with the difference that the unknown is the distribution $N^-(x)$.

In another formulation the decision is introduced as a term in the mortality coefficient in equations (81). In this case the collection process itself is no longer discrete, the yield is collected continuously. Leaving aside the question of the correctness of such a description of the yield collection (fishing) process (we will study it in Chap. VII), we note that we again obtain a linear programming problem with inequality constraints (all or some of the constraints in (100 - 103); there can also be other constraints) and one equality constraint of the type given in system (81).

Thus we arrive at the point where the problem decomposes into a series of linear programming problems, where the solution of one problem serves as the initial input for the next problem. Generally we should not expect that the solution obtained will be stationary in the most rigorous sense of this term. However, we can expect that as a result of solving successively such problems when the constraints on the number of individuals are satisfied, we will obtain conditions which can be called in some sense "stationary."

In conclusion we will give one way in which the constant c_0 can be selected in inequality (100).

It was shown in Section 1 of this chapter that the total population size $\bar{N}' = \int_0^{\infty} N(x) dx$ varies in accordance with the logistic

law.

But for such a model we fully solved the optimization problem in Chapter II. The decision is different from zero if and only if

$$\bar{N}^+ = \int_0^{\infty} N^+(x) dx > \frac{\bar{\alpha}}{\bar{\gamma} \left(e^{\frac{\bar{\alpha} h}{2}} + 1 \right)} = c_0. \quad (104)$$

Here we wrote the old results in the notation which we used in this chapter. We will now determine the quantities $\bar{\alpha}$ and $\bar{\gamma}$. To do this the function $\bar{N}(t)$ which was found from the solution of the averaged equation (82) is approximated by the logistic curve (this can be done since $\bar{N}(t)$ itself varies in accordance with the logistic law) and the parameter values obtained in the process are taken as the $\bar{\alpha}$ and $\bar{\gamma}$. In fact $\bar{\alpha}$ and $\bar{\gamma}$ are certain average values of the natality and mortality functions and also of the competitive ability function. /101

It can be shown that even if the inequality is satisfied with a properly chosen constant we have nondecreasing sizes; however, the yield collection procedure will distort the initial age distribution shifting it in the direction of the younger individuals and will decrease the mean age of the individuals in the population.

Many characteristics of individuals (for instance, size, weight, the biomass used, etc.) depend directly on age. On the other hand it is precisely these characteristics, not the age which determine the productive value of the individual or even the type of the decision used. For example, if fish are caught in nets, the decision in this case will be as follows: there exists a critical size of the individual which is determined by the dimension of the mesh which will catch all individuals whose size is larger or equal to the critical size without catching the remaining individuals. Here we have a typical example of a relay decision, whose "switching" points depend on a parameter such as the size. But since the size is directly correlated with the age of the individual, the problem can be formulated and solved in terms of the age structure of the population.

In the same way as in the preceding chapter, we can here formulate the problem of the "most valuable" population. It reduces to choosing from among all stationary distributions $N(x)$ which depend on the function $\gamma(x, y)$ that distribution which maximizes the functional

$$g(N) = \int_0^{\infty} \int_0^{\infty} c(x) N[x, \gamma] dx dy,$$

and to finding the corresponding $\gamma(x,y)$ which determines the trophic structure for the given system.

4. Optimization of the Age Structure of a Herd

A very interesting optimization problem for a model in which the age structure of the population was taken into account was formulated and solved by L. R. Ginzburg (Ginzburg, 1968). The concrete model which was studied was the model of an artificially cultivated population of a herd of large horned cattle.

For such system several types of optimization problem can be proposed, but all these involve the selection of some age distribution. The optimal policy for all such problems is the planned slaughtering of individuals in various age groups.

When the problems are formulated, in addition to the distribution of individuals by age, the sex of the individuals must also be taken into account. The system of equations for a population consisting of both sexes has the form

$$\left. \begin{aligned} \frac{dN_m}{dt} &= - \left[m_m(x) + \int_0^{\infty} \gamma_m(x, y) N_f(y, t) dy \right] N_m \\ \frac{dN_f}{dt} &= - \left[m_f(x) + \int_0^{\infty} \gamma_f(x, y) N_f(y, t) dy \right] N_f \\ N_m(0, t) &= \int_0^{\infty} n_m(x) N_f(x, y) dx \\ N_f(0, t) &= \int_0^{\infty} n_f(x) N_f(x, y) dx \\ N(x, t) &= N_m(x, t) + N_f(x, t) \end{aligned} \right\} \quad (105)$$

Here

$$\frac{d}{dt} = \frac{\partial}{\partial t} + \frac{\partial}{\partial x}.$$

The subscript "f" indicates that the parameter or the variable belongs to the female sex, and the subscript "m" indicates that it belongs to the male sex. The natural assumption is made in the model that the number of males in the population is adequate to fertilize all females.

1. The first type of problems are problems in which the optimal stationary age structure of the herd is determined. In this

case the number of head does not increase. In utilizing the herd two types of products are of value to us, milk and meat. It is easily seen that the decisions which optimize one type of product are by far not optimal for the other--we have a conflict situation.

We will make the following simplifying assumption:

a) we seek the stationary distribution

$$\frac{\partial N_m}{\partial t} = \frac{\partial N_f}{\partial t} = 0;$$

b) during reproduction the population is always in the logarithmic growth phase, so that terms with N_m^2 and N_f^2 in the right members of (105) can be ignored.

c) the number of individuals slaughtered is proportional to their number, so that the decision consists of changing the quantities m_m and m_f .

Under these assumptions the model system has the form:

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$$\left. \begin{aligned} \frac{dN_m}{dx} &= -[m_m(x) + k_m(x)] N_m \\ \frac{dN_f}{dx} &= -[m_f(x) + k_f(x)] N_f \\ N_m(0) &= \int_0^{\infty} n_m(x) N_f(x) dx \\ N_f(0) &= \int_0^{\infty} n_f(x) N_f(x) dx \end{aligned} \right\} \quad (106)$$

Here $k_m(x)$, $k_f(x)$ are admissible decisions which characterize the quantity slaughtered.

Let $v_m(x)$ and $v_f(x)$ be the quantity of marketable meat from males and females of age x , $l(x)$ be the milk production of cows of age x , $r(x)$ be the amount of milk consumed by calves of age x , $q_m(x)$ and $q_f(x)$ be the specific costs for maintaining one individual of age x . Let c_v and c_l be the unit costs for the meat and milk products. Then the meat production per unit time is equal to

$$V = c_v \int_0^{\infty} \left[v_m(x) \left(-\frac{dN_m}{dx} \right) + v_f(x) \left(-\frac{dN_f}{dx} \right) \right] dx. \quad (107)$$

The amount of marketable milk produced per unit time is equal to

$$L = c_l \int_0^{\infty} \{ l(x) N_f(x) - r(x) [N_m(x) + N_f(x)] \} dx. \quad (108)$$

The total cost incurred in keeping up the herd is expressed by the formula

$$Q = \int_0^{\infty} [q_m(x) N_m(x) + q_f(x) N_f(x)] dx. \quad (109)$$

In addition to the purely biological constraints given by (106) other constraints related to economic factors can also be given, for example, if the fodder resources are limited the following constraints can be imposed

$$\begin{aligned} \int_0^{\infty} u_{mi}(x) N_m(x) dx &\leq U_{mi}, \quad i = 1, 2, \dots, s, \\ \int_0^{\infty} u_{fj}(x) N_f(x) dx &\leq U_{fj}, \quad j = 1, 2, \dots, p. \end{aligned}$$

Here u_{mi} and u_{fj} is the amount of fodder of the i -th or j -th type used by individuals of age x per unit time, and U_{mi} and U_{fj} are the available stock of the corresponding fodders. One criterion which can be used in such a problem is maximizing the profit

$$I = V + L - Q.$$

If in all the formulas given above the integrals are replaced by finite sums and the derivatives by finite differences; this problem reduces to a typical linear programming problem (Dantzig, 1966).

We will give the results of the solution of the problem of the stationary age structure of the herd (in %) with the maximum

profit criterion, which is based on data from one of the Sovkhoz (State Farms) in the Leningradskaya Oblast'.

| | Calves in current year | Calves in previous year | Heifers | Cows | Young Bulls |
|---|------------------------------|-------------------------------|---------|------|----------------|
| Existed in 1967 | 19.2 | 13.6 | 9.8 | 53.0 | 4.4 |
| Calculated in ac- cordance with the maximum profit criterion | 16.1 | 10.0 | 6.1 | 59.8 | 8.0 |

The total increase in the profit for the optimal age structure is approximately 7%.

2. In the preceding problem it was assumed that all characteristics of the herd do not depend on time. This is a very strong constraint, since such characteristics as milk productivity are highly seasonal, and even though the remaining characteristics are less so, they nevertheless depend on time. Therefore, the problem of optimizing the periodic age structure arises naturally.

When we formulate the problem we abandon assumption a), and the problem becomes nonstationary. The basic equations of the model have the same form as in (106), but the first two equations must be written as

$$\left. \begin{aligned} \frac{\partial N_m}{\partial x} + \frac{\partial N_m}{\partial t} &= -[m_m(x) + k_m(x)] N_m \\ \frac{\partial N_f}{\partial x} + \frac{\partial N_f}{\partial t} &= -[m_f(x) + k_f(x)] N_f \end{aligned} \right\}$$

Certain constraints will depend on time. Exactly like the preceding problem, this problem reduces to a linear programming problem, but of large dimensionality. The criterion which is selected is the maximum profit over the entire period. Since the period selected is finite, the problem can be made discrete over time. The values of the quantities which depend on time are taken at the points at which the time interval is broken up, and the partial derivatives with respect to time are replaced by finite differences, which use the values of the variables at the points at which the interval was broken up.

3. Certain types of important problems are problems dealing with dynamic decision processes. How do such problems arise?

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Naturally the best state is the stationary or periodic age distribution which maximizes profit per unit time or per period, where the state of the system is such that it is fully restored at the beginning of the next period. Such problems already arose earlier when we were seeking optimal stationary yield collection processes in the BGC with the condition that they do not "deteriorate." Also here we can impose conditions that the number of individuals in some age group do not decrease (usually the reproductive part of the herd which makes further reproduction possible is preserved). Also other constraints of the "nondeterioration" type can be considered. For example, the condition that meat production should not decrease, due to certain planning restrictions. The criterion which is selected is maximum profit over the entire time interval under consideration.

This problem can be solved by dynamic programming methods. But the linearity of the problem and also the decisions as well as the constraints and the fact that the time interval is finite make it possible to reduce the problem to a linear programming problem.

It is natural that the results obtained from solving such problems are very approximate because of the coarseness of the initial model. Of course, it would also be desirable to take into account the genetic laws which determine some of the inherited characteristics during the reproduction, and the feeding regimen, which can be considered as a decision parameter, etc. But in the process the increasing difficulties which arise in the solution of such many-parameter problems are great, and the solution itself becomes so untractable, that one can doubt its usefulness.

5. Stationary Optimal Distributions

In preceeding paragraphs we already encountered problems in which the assumption that the age distribution is stationary was essential. However, many questions connected with their solution were not considered by us. We will fill this gap here on a number of very simple examples.

Let $c(x) \equiv 1$. Then the return will be the total number of individuals caught:

$$g(N^-, k) = \int_0^{\infty} k(x) \cdot N^-(x) dx. \quad (110)$$

As an additional condition, we will take a bound on the total size, the inequality (100). In the end we obtain the following problem:

find $k(x)$, which maximizes the function (110) subject to the constraints

$$\left. \begin{array}{l} \text{a) } 0 \leq k(x) \leq 1; \\ \text{б) } \int_0^{\infty} k(x) N^-(x) dx \leq \int_0^{\infty} N^-(x) dx - c_0. \end{array} \right\} \quad (111)$$

The initial distribution $N(x)$ is assumed to be given.

If $k(x) \equiv 1$, then in (111, б) $c_0 = 0$. If $c_0 > 0$, for example, the following $k(x)$ can be the optimal decisions (Fig. 35, а)

$$k(x) = \begin{cases} 0, & \text{if } 0 \leq x \leq a, \text{ where } a \text{ is determined from the condition:} \\ & \int_0^a N^-(x) dx \leq c_0; \\ 1, & \text{if } x > a. \end{cases} \quad (112)$$

It is clear that $k(x)$ is not unique. For example, the decision (Fig. 35, б):

$$k(x) = \begin{cases} 0, & \text{if } 0 \leq x \leq a_1, \text{ where } a_1 \text{ is determined from the condition:} \\ & \int_0^{a_1} N^-(x) dx = c_0 - b; \\ 1, & \text{if } a_1 \leq x \leq a_2, \text{ where } a_2 \text{ is determined from the condition:} \\ & \int_{a_1}^{\infty} N^-(x) dx = b; \\ 0, & \text{if } x > a_2. \end{cases}$$

will also be optimal.

In general any decision of the form:

$$k(x) = \begin{cases} 0 & \text{when } x \in E_0(x), \\ 1 & \text{when } x \in \bar{E}_0(x), \end{cases} \quad \begin{array}{l} \text{where the set } E_0 \text{ is determined from the} \\ \text{condition } \int_{E_0} N^-(x) dx = c_0; \\ \text{where } \bar{E}_0 \text{ is the complement of } E_0 \end{array}$$

will be optimal.

We will consider two successive stages in which a decision of the type (113) is made. Suppose that in the first stage we applied this decision for the given initial distribution. Then the form of the initial distribution in the second stage will depend essentially on the choice of the constant c_0 and the set E_0 . Clearly, E_0 must be chosen so that the remaining part of the population will reproduce the greatest possible number of offsprings at the next collection, and that it will have the smallest mortality. If the $x \in \bar{E}_0(x)$ coincide with the ages of sexual maturity and minimal mortality, then we can hardly expect a quick restoration of the size at the next collection stage. Of course, by appropriately choosing c_0 we can ensure that the total size will not decrease, but a more flexible decision is the selection of E_0 .

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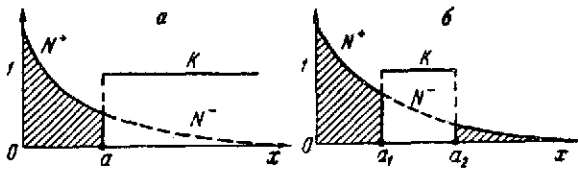


Fig. 35. Possible types of decisions.

The shaded region below the curve is the optimal age distribution, its area is exactly equal to the minimal total admissible population size.

This leads to the necessity of introducing still another condition, or to replacing (111) by another more realistic constraint, for example (102). Since in this case the increment in the population size is always bounded below by a positive constant, the condition that the total population size does not decrease is satisfied automatically.

Suppose now in (81) $dN/dt \equiv 0$, the natality and mortality functions depend only on x , and $\gamma(x,y)$ is small, so that the term which describes the competition can be ignored. Then (81) will be written in the form:

$$\frac{dN(x)}{dx} = -m(x)N(x); \quad N(0) = \int_0^{\infty} n(x)N(x)dx. \quad (114)$$

For the decision we will introduce $f(x)$, the rate at which the individuals of age x are caught. We will assume that the disturbances introduced by the fishing process (yield collection) are small, and that the process itself is equivalent to increasing the mortality among individuals of the corresponding age. Then the system with the decision will have the form

$$\frac{dN}{dx} = -mN - f(x); \quad N(0) = \int_0^{\infty} nN dx. \quad (115)$$

We formulate the problem of finding the $f(x)$ which maximizes the functional

$$g = \int_0^{\infty} c(x) f(x) dx. \quad (116)$$

As before we will assume that $c(x) \equiv 1$. If there are no constraints on $f(x)$ this problem has no solution. But it is completely natural to have a bound on $f(x)$ so that

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$$0 \leq f(x) \leq \bar{f}. \quad (117)$$

In addition to this a bound can be imposed, for example, on the total population size, so that

$$\int_0^{\infty} N(x) dx \geq c_0. \quad (118)$$

In contrast to the previous formulations, here we have a continuous collection process. While in the transition from one step to another the age distribution changed in jumps, now it is deformed continuously. The problem itself is formulated in such a way that by solving it we obtain the stationary (in the most rigorous sense of the word) age distribution.

Substituting the value of f which was found from (115) in the functional, we obtain

$$\begin{aligned}
g(\bar{f}) &= \int_0^{\infty} \left\{ -\frac{dN}{dx} - mN \right\} dx = N(0) - N(\infty) - \\
&\quad - \int_0^{\infty} mN dx = \int_0^{\infty} \{n(x) - m(x)\} N(x) dx = g(N).
\end{aligned}
\tag{119}$$

Here we made the very natural assumption that $N(\infty) = 0$.

We will now pass on to the bound for f . It follows from (117) that

$$0 \leq -\left\{ \frac{dN}{dx} + mN \right\} \leq \bar{f}. \tag{120}$$

This differential inequality is equivalent to the ordinary inequality:

$$N_0(x) \left\{ 1 - \frac{\bar{f}}{N_0(0)} \int_0^x \int_0^z m(\xi) d\xi dz \right\} \leq N(x) \leq N_0(x). \tag{121}$$

Here $N_0(x)$ is a solution of system (114), i.e., the initial age distribution. Since only nonnegative values of $N(x)$ make sense, letting

$$\bar{f} = \bar{f}(x) = N_0(0) \int_0^x \int_0^z m(\xi) d\xi dz,$$

we can write (121) in the form:

$$0 \leq N(x) \leq N_0(x). \tag{122}$$

Finally, we have: find the $N(x)$ which maximizes the functional /109

$$g(N) = \int_0^{\infty} \{n(x) - m(x)\} N(x) dx$$

subject to the constraints (118) and (122). When the solution to this problem is found, the unknown decision $f(x)$ is determined from (115). The optimal decision should be interpreted in the sense that at each instant it maximizes the total increment in the population size. To find the solution we shall use the Neyman-Pearson lemma.

We will determine the sets $E^-(\lambda)$, $E(\lambda)$, $E^+(\lambda)$ as follows:

$$\begin{cases} E^-(\lambda) = x & \text{with the condition that } n(x) - m(x) < \lambda; \\ E(\lambda) = x, & \text{" " " " } n(x) - m(x) = \lambda; \\ E^+(\lambda) = x & \text{" " " " } n(x) - m(x) > \lambda. \end{cases}$$

We define λ_0 as follows: λ_0 is the greatest lower bound of the set of all nonnegative λ which satisfy the inequality

$$\int_{E^+(\lambda)} N_0(x) dx \geq c_0.$$

The the set of optimal distributions $N(x)$ is determined from the relations:

$$N(x) = \begin{cases} N_0(x) & \text{on } E^+(\lambda_0); \\ 0 & \text{on } E^-(\lambda_0); \\ \text{is an arbitrary function defined on } E(\lambda_0) & \text{which} \\ \text{satisfies only conditions (118) and (122)} \end{cases}$$

For the concrete form of the natality and mortality functions plotted in Figs. 36a, b, c, we constructed the optimal distribution which is used to obtain from (115) the optimal decision $f(x)$. But here one difficulty arises: since when $f(x)$ is determined we must differentiate the distribution $N(x)$ which is a discontinuous function, dN/dx is not defined at the points of discontinuity, and consequently $f(x)$ is undefined. One way of overcoming this difficulty is "smoothing" the optimal distribution, i.e., approximating the discontinuous $N(x)$ by some continuous function for which the derivative exists everywhere. Another way is to introduce discrete age groups and to consider as the decision no longer the function $f(x)$ but the integral $\varphi_i = \int_{x_i}^{x_{i+1}} f(x) dx$.

where x_i , x_{i+1} are the boundaries of the age group. These can be

chosen in such a way, that all integrals are finite and only the number of individuals caught between ages x_i to x_{i+1} have meaning. We note that the values of $f(x)$ and φ_i which are obtained must be nonnegative. In the contrary case we set $\varphi(x) \equiv 0$ or $\varphi_i \equiv 0$. Figure 36, c shows the optimal decision $f(x)$ which corresponds to the distribution $N(x)$, plotted in Fig. 36, b. $N(x)$ was approximated by a continuous function.

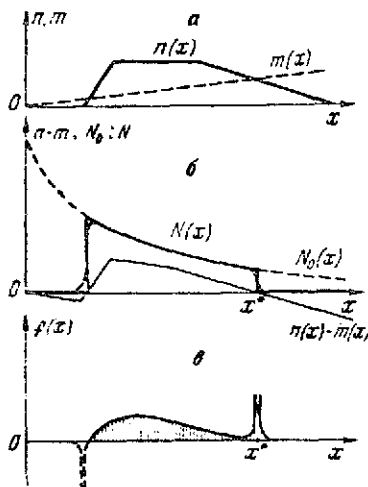


Fig. 36. Solution of the optimization problem for the continuous stationary catch.

a--form of natality and mortality functions; b--initial age distribution $N_0(x)$; optimal age distribution $N(x)$ (thick solid line); continuous approximation of optimum distribution (thick dotted line), curves m (mortality coefficient) and n (natality coefficient) on a scale 10 times larger than N_0 and N ; c--catch function $f(x)$. At the point x^* where $m(x) = n(x)$, $f(x^*) = \infty$. From a practical standpoint this means that all individuals of age x^* must be caught.

6. Distribution by Dimension. Relay Decisions Related to Specific Features of the Fishing Equipment. Consideration of Other Factors.

It is clear that the size of an individual is closely related to its age. Usually the older the individual the greater its size and biomass. Without dwelling now on various growth models (Thompson, 1917; Kostitzin, 1937) we will assume that we know the form of the function φ which describes the dependence of the size l of the individual on its age x , so that

$$l = \varphi(x). \quad (123)$$

Then equations (81) will be written in the form:

$$\left. \begin{aligned} \frac{\partial N}{\partial t} + \frac{d\varphi}{dx} \cdot \frac{\partial N}{\partial t} &= - \left\{ m(l) + \int_a^\infty \gamma(l, y) N(y, t) dy \right\} N(l, t) \\ N(a, t) &= \int_a^\infty \mu(l) N(l, t) dl; \quad N(l, 0) = g(l) \end{aligned} \right\} \quad (124)$$

where the natality, mortality, and competitive ability functions no longer depend on the age of the individual but on its size. Generally they can be given as functions of age, and recomputed, using (123) into sizes (a is the size of newly born individuals duals). /111

It can be seen from comparing (81) and (124), that the left members of the first equations differ by the factor $d\varphi/dx$ before the term dN/dl , otherwise the equations are identical. We expect that taking into account other factors will only slightly change the terms which contain the derivatives, the structure of the equations themselves will remain unchanged.

Suppose that we are given m factors x_1, x_2, \dots, x_m , each of which has its own distribution in the population. As a whole the population is described by the multidimensional function $N(x_1, \dots, x_m, t)$. Its meaning is the same as above, but now instead of a single factor, age, we also have other factors (size, fertility, etc.), and instead of a one-dimensional distribution a multidimensional distribution. Naturally, the natality, mortality and competitive ability functions may also depend on these on these variables. Suppose that we are given these factors as functions of time:

$$x_1 = \varphi_1(t); \quad x_2 = \varphi_2(t); \quad \dots, x_m = \varphi_m(t).$$

For example, if x_1 is age, $\varphi_1(t) = t$, since the age of an individual is equal to the time it lives. If the age is not measured in astronomical time units but in some other units, then $\varphi_1(t) \neq t$, and it is given by a more complex function.

We define the total derivative $N(x_1, \dots, x_m, t)$ with respect to time:

$$\frac{dN(x_1, \dots, x_m, t)}{dt} = \frac{\partial N}{\partial t} + \sum_{i=1}^m \frac{\partial N}{\partial x_i} \frac{\partial x_i}{\partial t} = \frac{\partial N}{\partial t} + \sum_{i=1}^m \frac{\partial N}{\partial x_i} \frac{d\varphi_i}{dt}. \quad (125)$$

Then the equation which describes the multidimensional distribution of sizes by these factors is written in the form:

$$\frac{dN}{dt} = - \left\{ m(x_1, \dots, x_m, t) + \int_{\Omega} \gamma(x_1, \dots, x_m, y_1, \dots, y_m, t) N \times \right. \\ \left. \times (y_1, \dots, y_m, t) d\omega \right\} N + R(N, x_1, \dots, x_m, t). \quad (126)$$

Here Ω is the region in which the x_1, \dots, x_m vary, $d\omega = dy_1 \dots dy_m$, $R(N, x_1, \dots, x_m, t)$ is a function which describes the increase in the population size due to birth, migration, etc. Often the increment is given not in terms of a function in the right member of the equation, but by a specially chosen boundary condition. For example, if x_1 is age, x_2 is the size of an individual, then $R \equiv 0$ and the increment in the number of individuals is determined from the boundary conditions: /112

$$a) \quad N(0, x_2, t) = \int_0^{\infty} n(x_1, x_2, t) N(x_1, x_2, t) dx_1;$$

$$b) \quad N(x_1, a, t) = \int_a^{\infty} n(x_1, x_2, t) N(x_1, x_2, t) dx_2.$$

In addition to the boundary conditions initial conditions must also be given. Of course, in this example a two-dimensional (more precisely three-dimensional since there is also a dependence on t) problem can be reduced easily to a one-dimensional problem because the size and age of an individual are related sufficiently rigorously, and $x_2 = \varphi_2(x_1)$ is a known function. Nevertheless, such a technique of increasing the dimensionality of the problem (known as "invariant imbedding") can be useful. Having found the solution of the problem in the entire region, $\Omega(t) = \{x_1, x_2, t\}$ we can easily obtain the solution which we need by studying the behavior of $N(x_1, x_2, t)$ along the curve $x_2 = \varphi_2(x_1)$.

If, for example, we take for x_2 the seasonal cost of an individual which, of course, depends on the age, we will no longer have such direct correlation. In this case the "invariant imbedding" method can yield good results. Since $x_2 = \varphi_2(x_1, t)$,

$$\left. \begin{aligned} & x_1 = t; \quad \frac{dx_1}{dt} = 1; \quad \frac{dx_2}{dt} = \frac{\partial \varphi_2}{\partial x_1} + \frac{\partial \varphi_2}{\partial t}; \\ & \text{and} \quad \frac{dN}{dt} = \frac{\partial N}{\partial t} + \frac{\partial N}{\partial x_1} + \left(\frac{\partial \varphi_2}{\partial x_1} + \frac{\partial \varphi_2}{\partial t} \right) \frac{\partial N}{\partial x_2}. \end{aligned} \right\} \quad (127)$$

Let us again return to the distribution by dimensions. It is clear that if we know how to find the age distribution, we can also find the distribution by dimensions. Therefore, all problems related to this distribution can be reformulated in terms of age distributions. In Section 3 of this chapter we considered the case when the specific features of the fishing equipment (fishing by nets with a certain mesh size) determines the type of decision. It represents a relay function with a single "switching" point. Since the dimension is related to the age, instead of the critical dimension l^* , we can determine the critical age x^* . If the decision is defined by the quantity $k(x)$, then

$$k(x) = \begin{cases} 0, & \text{for } 0 \leq x < x^*; \\ 1, & \text{for } x \geq x^*. \end{cases} \quad (128)$$

We no longer seek an optimizing function $k(x)$ or $f(x)$ but a number x^* which will maximize the functional

$$g(N, x^*) = \int_{x^*}^{\infty} c(x) N(x) dx; \quad (129)$$

subject to certain constraints, or a sequence of numbers x_i^* which /113 maximize the sum:

$$G = \sum_{i=1}^n \int_{x_i^*}^{\infty} c_i(x) N_i(x) dx. \quad (130)$$

All problems which were considered above are simplified considerably.

But besides such formulations also converse formulations are possible. For example if x^* is given, the problem consists of "selecting" the appropriate distribution $N(x)$. The same functionals (129) or (130) are maximized. But the maximizing

functions will then be $N(x)$, $N_1^-(x)$, on which various constraints can be imposed.

We will consider the maximization of the functional (129). If $N(x)$ is unbounded above, and $c(x) > 0$, the problem has no solution. Let

$$0 \leq N(x) \leq \bar{N}.$$

Then, the distribution:

$$N(x) = \bar{N} \text{ is optimal for all } x \geq x^*.$$

In order that the solution be meaningful we introduce additional constraints on $N(x)$, exactly as we did in the preceding chapters.

We thus conclude the chapter which was devoted to BGC optimization problems in whose models the ages, sizes, etc., of the individuals must be taken into account. This is usually necessary in optimization problems, because in the criterion function the difference in costs is taken into account as a function of the age or size of the individual caught. Of course, we only considered the simplest problems of this type. Undoubtedly, further study of these problems will yield many new and interesting results.

CHAP. VII. CONTINUOUS YIELD COLLECTION MODELS

Until now the continuous yield collection process was mainly considered as the limiting case of a discrete process (as $h \rightarrow 0$). From the very beginning despite the fact that the dynamics of the controlled system were described by differential equations in which time was continuous, we introduced the decisions as a discrete process. Strictly speaking, we did not need differential equations to describe the behavior of the system at all, we could have worked much more easily with difference equations. However, because of tradition we used differential equations, although, for example, in the study of stationary processes, the differential equations were replaced by difference equations. To a great extent this approach was determined by the methods which we used, the method of dynamic programming, which is much more conveniently applied in the discrete case. But we must not forget about powerful optimization methods which were specifically developed for continuous systems (for example, the Pontryagin maximum principle). In this chapter we will demonstrate the application of this principle to our specific problems.

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1. Continuous Collection Model in a Homogeneous Population.

Before we apply the maximum principle, we must set up correctly the model for the controlled system. Difficulties arise here, in particular the question of checking the model. We will solve this problem by a direct comparison of the results obtained from the model and by analyzing a discrete model as $h \rightarrow 0$. The discrete model itself is very simple in structure, therefore, we may expect that it is correct to some extent.

We will begin with a one-component BGC, a yield collection process which was studied in great detail in Chapter II.

We denote by $N(t)$ the population size, from which $q(t)$ individuals are removed at the instant t . The individuals which are removed participate neither in reproduction nor in competitive relations, so that the fundamental equation which describes the dynamics of the population size can be written in the form:

$$\frac{dN}{dt} = -q + (N - q)[\alpha - \gamma(N - q)], \quad (131)$$

with the natural constraint:

$$0 \leq q(t) \leq N(t). \quad (132)$$

Here α is the natural growth coefficient, γ is a coefficient which takes into account the competition among individuals.

In the given case $q(t)$ is an admissible control variable, and it characterizes the rate at which the yield is collected. If instead of q we introduce the variable k , which is related to q by the relation

$$q = kN, \quad (133)$$

constraint (132) can be rewritten in the form:

$$0 \leq k(t) \leq 1, \quad (134)$$

and the meaning of the new control variable is analogous to that introduced in Chapter II. However, for the time being we will not make this substitution. The criterion function in this case is written in the form: /115

$$G = \int_0^T q(t) dt + N(T). \quad (135)$$

The term $N(T)$ in (135) indicates, that the entire biomass is collected at the last instant T . If we consider G as a new variable, we can finally formulate the optimization problem of maximizing the yield collected as follows: Find

$$G^* = \max_{0 \leq q \leq N} G(t) | t = T; \quad (136)$$

subject to the conditions:

$$\left. \begin{aligned} \frac{dG}{dt} &= (N - q) \{ \alpha - \gamma (N - q) \} \\ \frac{dN}{dt} &= -q + (N - q) \{ \alpha - \gamma (N - q) \} \\ G(0) &= N(0) = N_0 \end{aligned} \right\} \quad (137)$$

In this formulation this problem becomes the so-called "open end problem" to which we will apply the "maximum principle" (Pontryagin, et al., 1961).

Often in problems of this type the yield function enters linearly, so that the fundamental equation has the form:

$$\frac{dN}{dt} = N(\alpha - \gamma N) - q(t) \quad (138)$$

and we formulate the problem of finding

$$\max_{0 \leq q \leq N} \int_0^T q(t) dt. \quad (139)$$

While the model described by (131) is equivalent by construction to the discrete model in Chapter II, model (138) is constructed altogether differently. If we consider (138) and (139) as an optimization problem, its solution is sufficiently simple: $q_{\text{opt}} = \bar{q}$, even though it is difficult to interpret from the biological point of view. Therefore, we proceed differently: we introduce various constraints, and $q(t)$ is sought taking into consideration these constraints. Such approach which we used in Sections 4, 5 of the preceding chapter enables us to obtain solutions which make better sense, but nevertheless a question which remains open is why these models yield different results. To answer this question we must analyze the way in which the models are constructed, and clarify the areas to which each of them is applicable.

2. Comparison of Two Types of Models

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We will consider the difference analogue of the first model. We will select as the time unit one step in the process and we will normalize appropriately the coefficients α and γ . Then at the instant t_i when the yield is collected

$$N^+(t_i) = N^-(t_i) - q(t_i). \quad (140)$$

If h is small, then with sufficient accuracy:

$$N^-(t_{i+1}) = N^+(t_i) + \alpha N^+(t_i) - \gamma [N^+(t_i)]^2. \quad (141)$$

Substituting (140) in (141), we obtain

$$N^-(t_{i+1}) = N^-(t_i) - q(t_i) + \alpha [N^-(t_i) - q(t_i)] - \gamma [N^-(t_i) - q(t_i)]^2. \quad (142)$$

Then, if the number of steps $n \gg 1$, and $N^-(t_{i+1}) - N^-(t_i)$ is sufficiently small, the solutions of equations (131) and (142) which are considered on a sufficiently large time interval, differ, on the average, by little. In this model the yield collection procedure affects in an essential way also propagation and intraspecific competition, since during the collection the individuals which actively participate in these processes are removed. In fact, it can be seen directly from (142) that the natural growth is not proportional to N , but to $N - q$, i.e. the number of remaining individuals. The same can also be said about the term which describes intraspecific competition.

We now pass on to the second model. We have for the population size at two successive instants of time (the yield is not collected):

$$N(t_{i+1}) = N(t_i) + \alpha N(t_i) - \gamma N^2(t_i). \quad (143)$$

If we remove slowly from the system a part of the individuals at the rate $q(t)$, so that this has no effect on the propagation or competition, then

$$N(t_{i+1}) = N(t_i) + \alpha N(t_i) - \gamma N^2(t_i) - q(t_i). \quad (144)$$

(138) is the differential analogue of (144). In fact the introduction of such a control variable is equivalent to increasing mortality in the population, without affecting essentially that part of the population which participates actively in the reproduction and competition processes.

The first model which is the limiting case of the discrete model, can be applied to describe a situation when the intervals between the collections are comparable in order of magnitude to the mean life of a generation or with the reproductive age (we can give as an example the yield collected in microbial coenoses or in artificial culture apparatus, hay making, pond fishing, etc.). On the other hand this model can be applied given any collection rate, even if the biomass is removed almost completely. The non-linearity, which is preserved in the transition from the discrete variant to the continuous model, makes it possible to take also into account such processes. /117

The second model is applicable when we make small but frequent catches in a population whose size is very large. Here the intervals between the catches must be much shorter than the mean life of a generation or the reproductive age (for example, fishing in large ocean or sea coenoses, slaughtering of cattle in dairy herds, etc.). This model is also applicable in other cases, with the condition that $q(t)$ is small compared to the total increment in the biomass. This implies immediately that such a model can be used when the population is in the logarithmic growth stage. This is easily verified.

The first model is a continuous approximation of a discrete process, the second model is continuous by construction and the assumptions on which it is based. It is interesting to note, that models which are very similar to the first model are widely used in economics to describe a production process, where a part of the product is used for expanding production and the part which makes up the return is completely removed from the system (as an

example we give the Markovitz model, many such models can be found in Gale's book, "Linear Economic Models") (1963).

Models of the second type are widely used to describe various automatic control systems in which the question of the possible optimization criteria is analyzed in detail.

Here we touched on an important problem dealing with the decision rules in a model which describes an "uncontrolled" system, i.e., a population or a BGC in which no yield is collected. At this point it is difficult to say anything about the advantages or disadvantages of a particular method which would allow us to make a choice immediately. We tend to favor the first model, since it preserves the nonlinearity of the decision. This leads us to expect "richer" solutions.

3. Solution of the Continuous Collection Problem

Let us return to problems (136), (137). We set up the Pontryagin function

$$H = (\psi_1 + \psi_0)(N - q)[\alpha - \gamma(N - q)] - \psi_1 q, \quad (145)$$

where the equations for ψ_0, ψ_1 have the form

$$\left. \begin{aligned} \frac{d\psi_0}{dt} &= 0; \\ \frac{d\psi_1}{dt} &= -\frac{\partial H}{\partial N} = \psi_1; \\ \psi_0(T) &= 1; \quad \psi_1(T) = 0; \end{aligned} \right\} \quad (146)$$

which implies immediately that

$$\psi_0 \equiv 1; \quad \psi_1 \equiv 0. \quad (147)$$

From the condition $dH/dq = 0$ and from (147) we have:

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$$q(t) = N(t) - \frac{\alpha}{2\gamma}. \quad (148)$$

Since $0 \leq q \leq N$, the optimal control will have the form:

$$q(t) = \begin{cases} N(t) - \frac{\alpha}{2\gamma} & \text{when } N(t) \geq \frac{\alpha}{2\gamma}; \\ 0 & \text{when } N(t) < \frac{\alpha}{2\gamma}. \end{cases} \quad (149)$$

Substituting the value $q(t)$ found in the criterion function, and assuming that $q(t) > 0$ almost everywhere on the interval $[0, T]$, we obtain

$$G^* = N(0) + \frac{\alpha^2}{4\gamma} T. \quad (150)$$

Comparing (149), (150) with formulas (6) and (10), we see that they coincide completely. Thus, the check confirms that we selected the correct model.

The equation which describes the change in the population size during the optimal collection has the form:

$$\frac{dN}{dt} = \begin{cases} \frac{\alpha^2}{4\gamma} + \frac{\alpha}{2\gamma} - N & \text{when } N(t) \geq \frac{\alpha}{2\gamma}; \\ N(\alpha - \gamma N) & \text{when } N(t) < \frac{\alpha}{\gamma}. \end{cases} \quad (151)$$

Let $N(0) \geq \alpha/2\gamma$. Integrating (151), we obtain:

$$N(t) = \left(\frac{\alpha^2}{4\gamma} + \frac{\alpha}{2\gamma} \right) (1 - e^{-t}) + N(0)e^{-t}. \quad (152)$$

We can easily see that for any t : $N(t) \geq \frac{\alpha}{2\gamma}$. Thus we have proved the continuous analogue of the proposition which was formulated for the discrete case, namely that if at some stage in the process the optimal control is different from zero, it will be different from zero in all successive stages.

When $t \rightarrow \infty$: $N(t) \rightarrow \frac{\alpha^2}{4\gamma} + \frac{\alpha}{2\gamma}$, so that for large t the process becomes stationary with a constant population size and the same control $q_\infty = \alpha^2/4\gamma$. If $N(0) = \frac{\alpha^2}{4\gamma} + \frac{\alpha}{2\gamma}$, the entire process is stationary, starting with $t = 0$, so that $N(t) - N(0) = 0$. Here we have some inconsistency with the discrete model, in which the initial condition which ensures stationarity as $h \rightarrow 0$, has the form $N_1^+ = \alpha/2\gamma$. In fact, however, there is no contradiction, since the trajectory which characterizes continuous collection

consists of points whose ordinates are equal to the sizes of the population attained in unit time, with the condition that no collection takes place. The initial sizes are determined by the points which lie on the curve.

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$$N'(t) = \frac{\alpha}{2\gamma} (1 - e^{-t}) + N'(0) e^{-t}, \quad (153)$$

which is the continuous approximation of the discrete collection process (the lower envelope of the "saw-tooth" plotted in Fig. 5, with the condition that the number of "teeth" tends to infinity, and their width tends to zero).

When we derived (131) we assumed that time is measured in dimensionless units, so that the ordinary time $\tau = th$ and all coefficients have been recomputed appropriately. Then, if $\bar{\alpha}$ and $\bar{\gamma}$, are coefficients referred to ordinary time, (131) can be written in the form

$$h \frac{dN}{d\tau} = (N - q) [\bar{\alpha}h - \bar{\gamma}h(N - q)] - q. \quad (154)$$

where q_{opt} is determined as before by formula (149). The solution of (154) when $q = q_{\text{opt}}$ is:

$$N(\tau) = \left(\frac{\bar{\alpha}h}{4\bar{\gamma}} + \frac{\bar{\alpha}}{2\bar{\gamma}} \right) (1 - e^{-\tau/h}) + N(0) e^{-\tau/h}. \quad (155)$$

As $h \rightarrow 0$: $N(\tau) \rightarrow \bar{\alpha}/2\bar{\gamma} = \alpha/2\gamma$. But $\tau = th$, and in order that τ be finite as $h \rightarrow 0$, it is necessary that $t \rightarrow \infty$, i.e., the number of steps must tend to infinity.

Making this type of transformation, which brings us from dimensionless time to time measured in ordinary units, we obtain the law for the change in the population size: $N(\tau) = \frac{\alpha}{2\gamma} = \text{const}$, which is independent of the initial condition (we assumed above that $N(0) \geq \alpha/2\gamma$ and $q(\tau) > 0$). Above we have shown that the transition process always takes place in a finite number of steps. It is clear that as $h \rightarrow 0$, this time interval shrinks to a point, and the process is stationary from the very beginning. The quantity $N(\tau) = \alpha/2\gamma$ is the real population size, since the entire increment above this quantity is collected. In a continuous collection process the population size function actually recorded is either the lower envelope of the "saw-tooth" or a curve which lies somewhat higher, but never the upper envelope. The control here is made on the lower level, it must never be less than $\alpha/2\gamma$, if this happens all intervention must cease until the population

again reaches this critical size.

If the collection process is discrete with a sufficiently large step during which the necessary measurements can be made, the control can be made both on the lower and upper level. But even here it is preferable to have the larger population size before the collection instant (upper level), since this instant is determined from it. Even in the case when this instant occurred astronomically, and the required upper bound has not yet been reached, it is better to wait until it is reached than to collect a smaller yield.

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Here we touched slightly on a very important problem, namely the relation between the optimal control and the information needed to make it (the so-called "observability" of the object). Unfortunately, this wide ranging and important problem is beyond the scope of our book.

4. Generalization for an Arbitrary Number of Species

Suppose that the BGC studied consists of n species and is described by the following system:

$$\frac{dN_i}{dt} = N_i \left(\varepsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right); \quad i, j = 1, 2, \dots, n. \quad (156)$$

Analogously, as we did for a one-component BGC, we introduce the control variables q_i ($i = 1, 2, \dots, n$), the number of individuals from the i -th species removed from the BGC at the instant t . Introducing these control variables in the original system (156), we obtain:

$$\frac{dN_i}{dt} = (N_i - q_i) \left\{ \varepsilon_i - \sum_{j=1}^n \gamma_{ij} (N_j - q_j) \right\} - q_i(t). \quad (157)$$

The natural constraints on $q_i(t)$ are:

$$0 \leq q_i(t) \leq N_i(t). \quad (158)$$

We introduce the variables $z_i(t)$:

$$\frac{dz_i}{dt} = q_i(t) + \frac{dN_i}{dt} \quad (159)$$

or

$$z_i(t) = \int_0^t q_i(\tau) d\tau + N_i(t). \quad (160)$$

If we denote by c_i the unit cost per individual or per unit biomass of the i -th species, then the requirement that the return be a maximum at the instant $t = T$ is written in the form:

$$G^* = \max_{0 \leq q_i \leq N_i} \sum_{i=1}^n c_i z_i(t) |_{t=T}; \quad (161)$$

subject to the conditions (157), (159) or (160). It is assumed that the c_i are independent of time. If this relation exists, then /121 instead of the variables $z_i(t)$ we must introduce the variables

$$\tilde{z}_i(t) = \int_0^t c_i(\tau) q_i(\tau) d\tau + c_i(t) N_i(t)$$

and

$$G(t) = \sum_{i=1}^n \tilde{z}_i(t).$$

We shall not do this in order not to make the problem more complex. Let $\xi_i = N_i - q_i$. Then the problem can be written in the form:
Find:

$$G^* = \max_{0 \leq q_i \leq N_i} \left\{ \sum_{i=1}^n \left[c_i \left(\int_0^T q_i(t) dt + N_i(T) \right) \right] \right\}; \quad (162)$$

with

$$\left. \begin{aligned} \frac{dQ}{dt} &= \sum_{i=1}^n c_i \xi_i \left(\varepsilon_i - \sum_{j=1}^n \gamma_{ij} \xi_j \right); \\ \frac{dN_i}{dt} &= \xi_i \left(\varepsilon_i - \sum_{j=1}^n \gamma_{ij} \xi_j \right) - q_i; \\ 0 &\leq \xi_i \leq N_i; \quad i, j = 1, 2, \dots, n. \end{aligned} \right\} \quad (163)$$

The initial conditions for this system are given.

We will use the "maximum principle" to solve the problem.
We set up the Pontryagin function:

$$H = \sum_{i=1}^n \left\{ \left[(c_i \psi_0 + \psi_i) \xi_i \left(e_i - \sum_{j=1}^n \gamma_{ij} \xi_j \right) \right] - q_i \psi_i \right\}. \quad (164)$$

The necessary conditions for the extremum H are:

$$\frac{\partial H}{\partial q_i} = -\frac{\partial H}{\partial \xi_i} - \psi_i = 0; \quad i = 1, 2, \dots, n. \quad (165)$$

We write down the equations for the ψ_i :

$$\frac{d\psi_i}{dt} = -\frac{\partial H}{\partial N_i} = -\frac{\partial H}{\partial \xi_i}; \quad i = 1, 2, \dots, n.$$

Taking into consideration (165), we will have

$$\frac{d\psi_i}{dt} = \psi_i; \quad \text{or} \quad \psi_i = \psi_i(0) e^t; \quad i = 1, 2, \dots, n. \quad (166)$$

Since for "an open end problem" $\psi_0(T) = \psi(t) = 1$,

$$\psi_i(T) = 0, \quad \text{so that} \quad \psi_i(t) = 0; \quad i = 1, 2, \dots, n.$$

Then

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$$H = \sum_{i=1}^n c_i \xi_i \left(e_i - \sum_{j=1}^n \gamma_{ij} \xi_j \right). \quad (167)$$

and

$$\frac{\partial H}{\partial q_i} = -\frac{\partial H}{\partial \xi_i} = \sum_{j=1}^n (c_i \gamma_{ij} + c_j \gamma_{ji}) \xi_j - c_i e_i.$$

Hence,

$$q_i(t) = N_i(t) - \xi_i; \quad i = 1, 2, \dots, n; \quad (168)$$

where the ξ_i are determined by solving the system of linear algebraic equations:

$$\sum_{j=1}^n (c_i \gamma_{ij} + c_j \gamma_{ji}) \xi_j = c_i e_i; \quad i = 1, 2, \dots, n. \quad (169)$$

If $\xi_i \geq 0$ and $N_i(t) \geq \xi_i$, formula (168) determines the optimal controls. If some $\xi_i < 0$ and for some t , $N_j(t) \leq \xi_j$, the optimal controls are determined from the formula:

$$q_i(t) = \begin{cases} N_i(t) - \xi_i & \text{when } N_i \geq \xi_i \geq 0; \\ N_i(t); & \text{when } \xi_i < 0; \\ 0; & \text{when } N_i < \xi_i. \end{cases} \quad (170)$$

Until now all our actions were determined by the "maximum principle" formalism and we were not interested in the question of interpreting the decision rules which were obtained formally.

5. Continuous Yield Collection in a "Predator-Prey" System

Let us return to the BGC model of the "predator-prey" type which we already know well (for the time being of the Volterra type). Then in (156) $n = 2$, $\gamma_{11} = \gamma_{22} = 0$, $\gamma_{12} = -\gamma_{21} > 0$, $e_1 > 0$, $e_2 < 0$. (For a comparison with the results in Chap. III, we will assume that $e_2 > 0$, and change accordingly the sign in the equation for N_2 .) Solving (169) for this concrete type, we obtain

$$\xi_1 = -\frac{c_2 e_1}{\gamma_{12} (c_1 - c_2)}; \quad \xi_2 = \frac{c_1 e_1}{\gamma_{12} (c_1 - c_2)}. \quad (171)$$

If $c_1 < c_2$, then $\xi_1 > 0$, $\xi_2 < 0$, and according to (170), the optimal controls are:

$$q_1 = N_1; \quad q_2 = \begin{cases} N_2 - \xi_2 & \text{when } N_2 \geq \xi_2; \\ 0 & \text{when } N_2 < \xi_2. \end{cases} \quad (172)$$

Substituting (172) in (157), and taking into account the assumptions which were made, we obtain the equations for determining the optimal trajectory

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$$\frac{dN_1}{dt} = -N_1; \quad \frac{dN_2}{dt} = \begin{cases} -e_2 \xi_2 + \xi_2 - N_2 & \text{when } N_2 \geq \xi_2; \\ -e_2 N_2 & \text{when } N_2 < \xi_2. \end{cases} \quad (173)$$

If $c_1 < c_2$, then $\xi_1 > 0$, $\xi_2 < 0$ and

$$q_1 = \begin{cases} N_1 - \xi_1 & \text{when } N_1 \geq \xi_1; \\ 0 & \text{when } N_1 < \xi_1; \end{cases} \quad q_2 = N_2; \quad (174)$$

$$\frac{dN_1}{dt} = \begin{cases} e_1 \xi_1 + \xi_1 - N_1 & \text{when } N_1 \geq \xi_1; \\ e_1 N_1 & \text{when } N_1 < \xi_1; \end{cases} \quad \frac{dN_2}{dt} = -N_2. \quad (175)$$

What are the optimal yield collection policies in such a system? If the "prey" are valued higher than the "predators" then as we can see from (172), (173), the optimal state is one in which the number of both "predators" and "prey" is held on the lowest level. The yield which is collected are almost all "prey," and when a certain level is exceeded, a certain number of "predators." If their number is below this level, they are not removed from the BGC. Under the action of such a decision the system makes a transition into ever increasing cycles. An analogous picture was also obtained for the discrete process where the problem was solved using the dynamic programming method (Chap. III, Sec. 2).

If the "predators" are valued higher, it follows from (174) and (175) that when optimal control is applied, the number of "predators" is held on the lowest possible level (the yield caught are almost all "predators"). "Prey" are either not collected at all or their number is below a certain level, or only a certain fraction is collected. Sooner or later their number is equal to $(N_1)_\infty = (e_1 + 1) \xi_1$, and does not change

further, and the number of "prey" collected is $(q_1)_\infty = \epsilon_1 \xi_1$.

Under the action of such control the system also makes a transition into ever increasing cycles, which, however, are bounded above by the line $N_1 = (\epsilon_1 + 1) \xi_1$. The point which is plotted moving along this line tends to occupy a position with the smallest possible coordinate N_2 . The picture was analogous for the discrete model. All that was said above is another proof that for a "predator-prey" system described by the classical Volterra model we cannot obtain an optimal stationary process (without imposing constraints which were selected in a certain way). As we have already shown a stationary process occurs only when a finite step of the process is selected uniquely, which, of course, is impossible when a continuous collection model is used.

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If we introduce in the system sufficiently strong damping, i.e., if we assume that $\gamma_{11}, \gamma_{22} \gg 0$, we obtain a model which we called the Kostitzin model. It follows immediately from (169) and (170) that the optimal control is determined from formula (170), where $n = 2$, and the quantities ξ_1 and ξ_2 are equal to:

$$\left. \begin{aligned} \xi_1 &= \frac{2c_1 c_2 \epsilon_1 \gamma_{22} + c_2 (c_1 - c_2) \epsilon_2 \gamma_{12}}{4c_1 c_2 \gamma_{11} \gamma_{22} - (c_1 - c_2)^2 \gamma_{12}^2} \\ \xi_2 &= - \frac{2c_1 c_2 \epsilon_2 \gamma_{11} + c_1 (c_1 - c_2) \epsilon_1 \gamma_{12}}{4c_1 c_2 \gamma_{11} \gamma_{22} - (c_1 - c_2)^2 \gamma_{12}^2} \end{aligned} \right\} \quad (176)$$

Here we assume as before that $\gamma_{12} = -\gamma_{21} > 0$, $\delta_2 > 0$. Suppose that ξ_1 and ξ_2 are positive. Then we may expect that the controls q_1 and q_2 will be more interesting than in the preceding case. But first of all it is necessary that $c_1 \neq c_2$. If $c_1 = c_2$,

$$\xi_1 = \frac{\epsilon_1}{2\gamma_{11}} > 0; \quad \xi_2 = -\frac{\epsilon_2}{2\gamma_{22}} < 0;$$

so that $q_2 = N_2$ and $\frac{dN_2}{dt} = -N_2$. This means that when the costs are equal, the greatest possible extermination of the "predators" is optimal, a realistic result. The two extreme cases when $c_1 = 0$, $c_2 > 0$ or $c_2 = 0$, $c_1 > 0$ are not very interesting, since they yield approximately the same results as the Volterra model with $c_2 > c_1$ and $c_1 > c_2$.

Suppose that $c_1, c_2 > 0$, $c_1 \neq c_2$ (if $\gamma_{12} \neq -\gamma_{21}$, we can ignore the last constraint and replace it by $c_1 \gamma_{12} \neq -c_2 \gamma_{21}$). Since we are considering a strongly damped system so that γ_{12} is small compared to γ_{11} and γ_{22} , we can assume that

$$4c_1c_2\gamma_{11}\gamma_{22} > (c_1 - c_2)^2 \gamma_{12}^2. \quad (177)$$

Below we shall consider the case when the reversed inequality holds. If $c_1 > c_2$, then $\xi_2 < 0$, and the optimal control for the "predators" is removing them as much as possible from the BGC. Suppose now that $c_2 > c_1$. Then, when

$$(c_2 - c_1)\varepsilon_1\gamma_{12} > 2c_2\varepsilon_2\gamma_{11} \quad (178)$$

$\xi_2 > 0$ and $q_2 < N_2$, i.e., the control for the "predators" is no longer their complete (or nearly complete) extermination. If

$$(c_2 - c_1)\varepsilon_2\gamma_{12} < 2c_1\varepsilon_1\gamma_{22}, \quad (179)$$

then also $\xi_1 > 0$ and, consequently, $q_1 < N_1$. This means that such cost ratios exist for which the optimal control lies within the feasible region $[0, N_1] \times \dots \times [0, N_n]$. The collection process itself which is determined by the initial conditions becomes stationary after a certain time. This is easily shown by writing out the equations which describe the optimal trajectory.

Let us return to inequality (178). We have shown above that /125 the system is stable when $\varepsilon_1\gamma_{12} > \varepsilon_2\gamma_{11}$. On the boundary of the stability region $\varepsilon_1\gamma_{12} = \varepsilon_2\gamma_{11}$ and it follows from (178) that $c_2 < c_1$. This is impossible since the costs are always positive. In order that (178) be satisfied the stability condition must be satisfied with a "margin." This "margin" is easily calculated. Let $c_2 = \lambda c_1$, where $\lambda > 1$ and $\varepsilon_1\gamma_{12} = \mu \varepsilon_{11}$, and where $\mu > 1$ determines the stability "margin." By substitution in (178) we obtain:

$$\mu > \frac{2\lambda}{\lambda - 1}. \quad (180)$$

On the other hand (179) implies that

$$\lambda < 1 + \frac{2\varepsilon_1\gamma_{22}}{\varepsilon_2\gamma_{12}}. \quad (181)$$

Thus, if the cost ratio $\lambda = \frac{c_2}{c_1}$ satisfies the following inequality

$$\frac{\varepsilon_2\gamma_{12} + 2\varepsilon_1\gamma_{22}}{\varepsilon_2\gamma_{12}} > \frac{c_2}{c_1} > \frac{\varepsilon_1\gamma_{12}}{\varepsilon_1\gamma_{12} - 2\varepsilon_2\gamma_{11}}, \quad (182)$$

the optimal controls lie within the feasible region (for some $t \in [0, T]$ they can be zero). To make such a situation possible, the parameters of the system must satisfy the inequality

$$(\varepsilon_2\gamma_{12} + 2\varepsilon_1\gamma_{22})(\varepsilon_1\gamma_{12} - 2\varepsilon_2\gamma_{11}) > \varepsilon_1\varepsilon_2\gamma_{12}^2. \quad (183)$$

It is always satisfied if the system (156) has a stable node when $n = 2$.

We note that (177) follows immediately from (178) and (179). Therefore inequality (177) can be ignored since it is not essential. If

$$\left. \begin{aligned} (c_2 - c_1)\varepsilon_1\gamma_{12} &< 2c_2\varepsilon_2\gamma_{11} \\ (c_2 - c_1)\varepsilon_2\gamma_{12} &> 2c_1\varepsilon_1\gamma_{22} \end{aligned} \right\}, \quad (184)$$

$c_1c_2\gamma_{11}\gamma_{22} < (c_1 - c_2)^2\gamma_{12}^2$ and when $c_2 > c_1$, the quantities ξ_2 and ξ_2 are positive. The analogues of inequalities (180 - 182) will have the same form only their signs will be reversed. It can be assumed that the reversed inequality (183) is satisfied in the case when system (156) has oscillatory solutions. For the Volterra model instead of inequality (183) and the reversed inequality, we will have the identity: $\varepsilon_1\varepsilon_2\gamma_{12}^2 = \varepsilon_1\varepsilon_2\gamma_{12}^2$. The inequality (182) and its analogue become the equality $c_2 = c_1$.

We will write the equations for the criterion function. In a Volterra model:

$$\frac{dG}{dt} = \begin{cases} -c_2\varepsilon_2p_2 & \text{when } c_1 > c_2; \\ c_1\varepsilon_1p_1 & \text{when } c_1 < c_2. \end{cases} \quad p_i = \begin{cases} \xi_i & \text{when } N_i > \xi_i; \\ N_i & \text{when } N_i < \xi_i. \end{cases} \quad i = 1, 2.$$

This confirms the earlier result that when $c_1 > c_2$ the return consists of the "prey" and "predators," which were collected in the beginning of the process. Continuing the collection can only decrease the return ($dG/dt < 0$). If $c_2 > c_1$, the return consists only of "prey" which is collected in the yield collection process. The return itself increases over time, since $dG/dt > 0$.

In the Kostitzin model when the corresponding inequalities are satisfied, ξ_1 and ξ_2 are positive and

$$\frac{dG}{dt} = c_1 \gamma_{11} \xi_1^2 + (c_1 - c_2) \gamma_{12} \xi_1 \xi_2 + c_2 \gamma_{22} \xi_2^2. \quad (185)$$

If inequality (177) is satisfied, then for any ξ_1, ξ_2 : $\frac{dG}{dt} > 0$.

If the reversed inequality is satisfied, then $dG/dt > 0$ in the regions determined by the inequalities (Fig. 37):

$$\left. \begin{aligned} \Omega_1: 0 < \xi_1 < \xi_2 & \left\{ \frac{(c_2 - c_1) \gamma_{12} - \sqrt{(c_2 - c_1)^2 \gamma_{12}^2 - 4c_1 c_2 \gamma_{11} \gamma_{22}}}{2c_1 \gamma_{11}} \right\} \\ \Omega_{11}: 0 < \xi_2 < \xi_1 & \left\{ \frac{2c_1 \gamma_{11}}{(c_2 - c_1) \gamma_{12} + \sqrt{(c_2 - c_1)^2 \gamma_{12}^2 - 4c_1 c_2 \gamma_{11} \gamma_{22}}} \right\} \end{aligned} \right\} \quad (186)$$

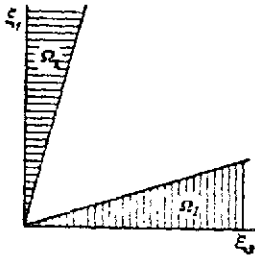


Fig. 37. Range of admissible values for ξ_1 and ξ_2 (shaded)

Substituting in (186) the values of ξ_1 and ξ_2 from (185), and solving these inequalities for c_2/c_1 , we obtain additional bounds on the costs (in addition to the reversed inequalities (182)). We note these are more rigorous bounds than those generated by the requirement that the ξ_1 and ξ_2 be positive. Thus, if the costs and the parameters of the system satisfy the reversed inequality (177), the solution makes sense (the return increases over time) not for any positive ξ_1 and ξ_2 , but only for those in

region Ω_I or Ω_{II} .

We did not consider upper bounds on ξ_1 and ξ_2 , since these are taken into account in the equations themselves. Since ξ_1, ξ_2 depend only on the parameters of the system and on the costs, when these quantities are constant, the ξ_1, ξ_2 will also be constant. Therefore, it suffices to choose $N_i(0) \geq \xi_i$ in order that for any t : $N_2(t) \geq \xi_i, i = 1, 2$. In general, for any n , not only for $n = 2$, when the initial conditions are selected appropriately $N_i(t) \geq \xi_i$, $q_i(t) \geq 0, i = 1, \dots, n$. In fact, since ξ_i is independent of time, $\xi_i = N_i(t) - q_i(t) = N_i(0) - q_i(0)$, and when $\xi_i \leq N_i(0)$ is chosen, for any t : $N_i(t) \geq \xi_i, i = 1, 2, \dots, n$. Taking this into account (170) can be written in the form: /127

$$q_i(t) = \begin{cases} N_i(t) - \xi_i & \text{when } \xi_i \geq 0; \\ N_i(t) & \text{when } \xi_i < 0. \end{cases} \quad (187)$$

$i = 1, 2, \dots, n$

with the condition $N_i(0) \geq \xi_i$. If even for one $N_k, N_k(0) < \xi_k$, then $q_k = 0$ until for some $t = t^*, N_k(t^*) \geq \xi_k$. Then for $t > t^*, N_k(t) \geq \xi_k$.

6. Species Which Compete Among Themselves

Suppose that we have a BGC consisting of n competing species. We assume for simplicity that $\gamma_{ij} = \gamma_{ji}, i, j = 1, 2, \dots, n$. The BGC will be described by system (156) where all $\epsilon_i, \gamma_{ij} > 0$. The optimal control vector $\vec{q}\{q_1, q_2, \dots, q_n\}$ is determined from formula (170), in which the ξ_i are found from the equations:

$$\sum_{j=1}^n \gamma_{ij}(c_i + c_j)\xi_j = c_i \epsilon_i; \quad i = 1, 2, \dots, n. \quad (188)$$

If $c_i = c$ for all i ,

$$\sum_{j=1}^n 2\gamma_{ij}\xi_j = \epsilon_i; \quad i = 1, 2, \dots, n;$$

and $\xi_i = \frac{1}{2} \tilde{N}_i$, where \tilde{N}_i is the stationary state in the BGC. Since the \tilde{N}_i must be positive (by definition of the problem the sizes cannot be negative, and moreover the positiveness of \tilde{N}_i together with the positiveness of the determinant of the matrix $\| \gamma_{ij} \|$ and its principal minors ensure their stability), all $\xi_i > 0$, and the optimum control is:

$$q_i = \begin{cases} N_i - \frac{1}{2} \tilde{N}_i & \text{when } N_i \geq \frac{1}{2} \tilde{N}_i; \\ 0 & \text{when } N_i < \frac{1}{2} \tilde{N}_i. \end{cases} \quad (189)$$

$i = 1, 2, \dots, n.$

This control makes it possible to collect in a given time the maximum biomass of all species which make up the BGC. For each individual species the control coincides with that obtained in Chapter 4 for a one-component BGC, where also $\xi = \frac{1}{2} \tilde{N}$.

Summing all equations (156) in which $\gamma_{ij} = \gamma_{ji}$, we obtain an equation which describes the dynamics of the total biomass of the BGC (we will denote it by M):

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$$\frac{dM}{dt} = \sum_{i=1}^n \varepsilon_i N_i - \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} N_i N_j. \quad (190)$$

We will find the point $\{N_1^*, \dots, N_n^*\}$ at which dM/dt attains a maximum. Differentiating the right member of (190) with respect to the N_i and setting the derivatives equal to zero, we obtain

$$\sum_{j=1}^n 2\gamma_{ij} N_j^* = \varepsilon_i; \quad i = 1, 2, \dots, n. \quad (191)$$

But system (191) is the same as the system from which the ξ_i are determined, where $c_i = c$, so that $\xi_i = N_i^*$. Since $q_i = N_i - \xi_i$ (when $\xi_i \leq N_i$), $q_i = N_i - N_i^*$ (when $N_i \geq N_i^*$). This means that the optimal yield collection policy will be as follows (for the maximum collected biomass criterion): the system is held in the state for which the total increase in the biomass is a maximum and the yield collected is the "incremental" biomass above this level

which is determined from (191).

The case when $c_1 \neq c_2$ is studied most conveniently when $n = 2$. Then

$$\left. \begin{aligned} \xi_1 &= \frac{2c_1c_2\epsilon_1\gamma_{22} - (c_1 + c_2)c_2\epsilon_2\gamma_{12}}{4c_1c_2\gamma_{11}\gamma_{22} - (c_1 + c_2)^2\gamma_{12}^2} \\ \xi_2 &= \frac{2c_1c_2\epsilon_2\gamma_{11} - (c_1 + c_2)c_1\epsilon_1\gamma_{12}}{4c_1c_2\gamma_{11}\gamma_{22} - (c_1 + c_2)^2\gamma_{12}^2} \end{aligned} \right\} \quad (192)$$

In order that ξ_1 and ξ_2 be positive, it is sufficient that the numerators of the fractions in (192) have the same sign, since when the numerators are positive, the denominator is also positive, and vice versa. We will write the equation for the return:

$$\frac{dG}{dt} = c_1\gamma_{11}\xi_1^2 + (c_1 + c_2)\gamma_{12}\xi_1\xi_2 + c_2\gamma_{22}\xi_2^2. \quad (193)$$

It is easily seen that for any ξ_1 and ξ_2 : $dG/dt \geq 0$.

The difference in the costs only displaces the level above which the increment is removed as the yield. Suppose that $c_1 < c_2$. We will consider the extreme case $c_1 = 0$. Then $\xi_1 = \epsilon_1/\gamma_{12}$, $\xi_2 = 0$. This means that in the second species the increment is removed completely and that the number of individuals in the species itself is held at a minimum; the first species is maintained on a level which depends only on the natural growth coefficient of the second species and on the coefficient which describes the competition between them.

7. Optimal Yield Collection for a General Model

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Suppose that the dynamics of the biogeocoenosis are described by the system

$$\begin{aligned} \frac{dN_i}{dt} &= f_i(N_j, \alpha_k), \\ i, j &= 1, 2, \dots, n, \quad k = 1, 2, \dots, p, \end{aligned} \quad (194)$$

where α_k are certain parameters of the model which were selected in such a way that the unit of time is a dimensionless quantity.

System (194) with the control variables $q_i(t)$ will be written in the form:

$$\begin{aligned} \frac{dN_i}{dt} &= f_i(N_j - q_j, \alpha_k) - q_i, \\ i, j &= 1, 2, \dots, n, \quad k = 1, 2, \dots, p, \end{aligned} \quad (195)$$

where the q_i satisfy the conditions

$$0 \leq q_i(t) \leq N_i(t). \quad (196)$$

The problem of optimizing the total yield taking into account the unit cost of the biomass of the i -th species c_i will have the form:

Find

$$G^* = \max_{0 \leq q_i \leq N_i} \left\{ \sum_{i=1}^n c_i z_i(T) \right\} \quad (197)$$

with

$$\left. \begin{aligned} \frac{dG}{dt} &= \sum_{j=1}^n c_j f_j(\xi_l, \alpha_k) \\ \frac{dN_i}{dt} &= f_i(\xi_j, \alpha_k) - q_i \\ i, l &= 1, 2, \dots, n, \quad k = 1, 2, \dots, p \end{aligned} \right\} \quad (198)$$

and the initial condition

$$N_i(0) = N_{i0}; \quad G(0) = 0.$$

Here T is the time when the collection process ends:

$$\begin{aligned} z_i(t) &= \int_0^t q_i(\tau) d\tau + N_i(t); \\ \xi_i(t) &= N_i(t) - q_i(t). \end{aligned}$$

Using for the solution of the problem the Pontryagin "maximum principle" we obtain at the point which we "suspect" to be the extremum

$$H = \sum_{i=1}^n c_i f_i(\tilde{x}_i, u_k). \quad (199)$$

$$\frac{\partial H}{\partial q_i} = -\frac{\partial H}{\partial \xi_i} = \sum_{i=1}^n c_i \frac{\partial f_i}{\partial \xi_i} = 0. \quad (200)$$

Relations (200) define a system of equations which are used to find the optimal values q_i ($i = 1, 2, \dots, n$).

If

$$f_i = N_i \left(\varepsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right), \quad i = 1, 2, \dots, n,$$

relations (200) will coincide with system (169), from which the optimal controls for the Volterra model of the BGC are found.

8. Maximum Yield Theorem

The total biomass of the biogeocoenosis is equal to

$$M = \sum_{i=1}^n N_i.$$

If every unit of the biomass or individuals relating to the i -th component of the BGC has a cost c_i assigned to it ($c_i = \text{const}$, $i = 1, 2, \dots, n$) then the total "cost" of the entire BGC can be written in the form

$$\overline{M}(t) = \sum_{i=1}^n c_i N_i(t). \quad (201)$$

Differentiating (201) with respect to t , and using relations (194) for the BGC which is not utilized, we obtain an equation which describes the change in the "cost" of the BGC:

$$\frac{d\bar{M}}{dt} = \sum_{i=1}^n c_i f_i(N_i). \quad (202)$$

It is not difficult to find the point at which $d\bar{M}/dt$ attains a maximum. This point $\{N_i^*\}$, ($i = 1, 2, \dots, n$) will be called the optimal state of the biosystem.

Differentiating (202) with respect to the N_j and equating the derivatives to zero, we obtain

$$\sum_{i=1}^n c_i \frac{\partial f_i}{\partial N_j} = 0, \quad j = 1, 2, \dots, n. \quad (203)$$

But system (203) when N_i is replaced by ξ_i is identical with /131 system (200), from which the optimal controls are found. Further, since for the optimal values q_i^* the function H takes on a maximum, then for quantities which are defined analogously, the "cost" of the BGC also attains a maximum value. It follows from the identity that

$$N_i^* = \xi_i^* = N_i - q_i^*, \\ i = 1, 2, \dots, n$$

and

$$q_i^* = N_i - N_i^*.$$

This means that the state in which the increment in the "cost" of the BGC (the increment in the "weighted" biomass) is a maximum is optimal. The yield which is removed is the entire "incremental" biomass above the level determined by this state. If the biomass or the number of individuals in some component of the BGC is below this level, it must not be collected until this level is reached.

These results can be obtained directly from formula (199) which defines H . If in this formula the ξ_i are replaced by the N_i , then $H = \frac{d\bar{M}}{dt}$, and it follows from the "maximum principle" that

on the optimal trajectory $H^* = \max_{N(t)} H$. Thus, the state of the BGC with the largest derivative of \bar{M} with respect to time is the optimal state. We have thus proved the "maximum yield theorem" which can be formulated as follows:

When the yield is collected continuously, the optimal control in the biosystem will be such, that the biosystem arrives in a state in which the derivative $d\bar{M}/dt$ is a maximum, and then by collecting the yield, it is maintained in this state until the end of the process.

CHAP. VIII. STABILITY OF BIOLOGICAL ASSOCIATIONS.

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1. Stability and Variety in the Association

If we have a sufficiently "good" mathematical model of the biological association (in the sense that it is adequately and fully described), then the question of the stability of a real association can be answered by a study of our model using the usual methods of stability theory. The system will be stable if its trajectory in phase space does not go beyond the boundaries of a given region for certain finite perturbations of a sufficiently wide spectrum. We note that the entire problem can also be considered from the point of view of reliability theory (more precisely from what is usually called "the reliability of dynamic systems").

But in practice a study based on this approach is often not possible, since setting up a good model is an extremely difficult problem. Therefore, it is very tempting to find a function (or functional), whose value when it is calculated for a particular association could be used to make a judgment about the degree of its stability.

Among ecologists it is almost an axiom that the more complex in structure the associations the more stable they are. This leads to the idea of using as a measure of stability of the association information entropy (or some analogue). This idea was formulated for the first time most clearly by Margalef (Margalef, 1956) who proposed to use the so-called "diversity" for characterizing the association

$$D = -N \sum_{i=1}^n p_i \ln p_i, \quad (204)$$

where $p_i = \frac{N_i}{N}$; $N = \sum_{i=1}^n N_i$ is the number of individuals in the

i-th species in the association, and n is the number of species.

It is easily seen that the "diversity" differs from information entropy only by the factor N, the total size of the association.

According to MacArthur (MacArthur, 1955), the stability of the association can be characterized by the following quantity

$$S = - \sum_{i=1}^n p(s_i) \ln p(s_i), \quad (205)$$

where $p(s_i)$ is the probability that energy will be transferred over a definite path s_i .

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The larger the quantity S, the more stable the association. When this measure is used, the stability of the association is determined by the complexity of the structure of the trophic relations. Clearly the elimination of a particular type of species from the association and the destruction of the trophic relations which connect it with the remaining species has a smaller effect on an association with a large value of S than on one with a small value. The $p(s_i)$ themselves, in turn, depend on the number of species which make up the association.

It follows from everything that was said above, that the stability and diversity of the association are interrelated, so that a biosystem with greater diversity is more stable. This means that the quantity D can be used as a stability measure of the association.

Since it can be postulated that any system tends to a maximally stable state, the association must tend to a state with maximum diversity. Observations have shown that biological associations are characterized by a tendency to attain maximum sizes within the limits permitted by the external environment (for example, the population tends to fill to a maximum the entire habitat area). But it follows from (204) that for any internal structure of the association, the maximum value of D is attained for the greatest possible value of N, the total association size. This is a sufficiently weighty reason in favor of choosing the diversity D as a measure of stability.

2. Paradoxes Related to the Application of Various Analogues of Information Entropy As A Measure of Stability

What will be the most stable association if we use as the

criterion the quantity D or S? In other words for what values of N_i and for which structure of the trophic connections does D or S_i attain a maximum?

Since $\sum_{i=1}^n p_i = 1$, using the method of Lagrange multipliers, the necessary conditions for the maximum can be written in the form

$$\frac{\partial D'}{\partial p_i} = -N(\ln p_i + 1) + \lambda = 0, \quad i = 1, 2, \dots, n, \quad (206)$$

where

$$D' = -N \sum_{i=1}^n p_i \ln p_i + \lambda \left(\sum_{i=1}^n p_i - 1 \right).$$

Multiplying (206) by p_i and summing, we obtain

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$$\lambda = N \left(\sum_{i=1}^n p_i \ln p_i - 1 \right) = -D + N.$$

Substituting this expression in (206), we will have

$$\ln p_i = \sum_{j=1}^n p_j \ln p_j, \quad i = 1, 2, \dots, n. \quad (207)$$

It is easily seen that this equality is satisfied only when

$$p_i = p^* = \frac{1}{n} = \text{const}, \quad (208)$$

where D attains a maximum over the variables p_i at this point.

And finally the diversity of the association is a maximum if:

a) the total association size N is a maximum for the given conditions in the environment;

b) all species in the association are represented with equal frequency. Since N stabilizes sooner or later, the association must evolve to a state with $p_i^* = \text{const}$ for all species.

Thus, the most stable association is an association in which no

hierarchy of species exists, and all species are represented in equal proportions. But observations of real associations (in particular the most easily isolated elementary components of the biosphere, the biogeocoenosis) indicate something entirely different, namely that any association which existed for a sufficiently long time (hence, which is also stable) has a sharply pronounced hierarchial structure. Everything that was said above leads to the idea that using the diversity as a measure of stability of the association is not fully justified.

Turning to the measure S introduced by MacArthur, we see that it attains a maximum when $p(s_1) = p(s_2) = \dots$, i.e., in a most stable association the probability that any path over which energy is transferred will be selected is the same, so that any trophic connection is established with equal probability. Of course, such a structure is not hierarchial. Moreover, since the selection of any possible energy migration path is equiprobable, such system will not have any definite structure. All this contradicts observations which were made on real natural associations, and therefore the measure S is also unsatisfactory.

We note, however, that in many laboratory (and not only laboratory) associations, in the succession stage and during movement to a climax, increased diversities are actually observed. Apparently this measure characterizes to some extent the association, further, in all probability, it can even characterize the stability of the association, although not everywhere, i.e., only in the early succession stages. /135

What is the reason for these paradoxes? Apparently it is the formal application of the apparatus of information theory to systems to which it should not be applied. Just as Boltzman entropy in statistical physics, also information entropy in information theory makes only sense for sets consisting of weakly interacting particles or some other types of objects. The introduction of the entropy measure for such a set is fully justified (Khinchin, 1943). But as soon as we deal with systems whose elements strongly interact among themselves, the entropy measure is no longer satisfactory. And biogeocoenoses whose structure is mainly determined not by the characteristics of the species itself but by the characteristics of the interspecific relations, in which the competitive relations manifest themselves most strongly near equilibrium, are precisely systems with strong interactions.

From this point of view the applicability of the entropy measure at various succession stages is understandable. The point is that in these stages far from equilibrium, the competition is still weak, and the competitive pressures are small so that the biogeocoenosis can be considered as a system with weak interactions.

3. Stability of a Homogeneous Population

We will consider a model of a homogeneous population in the environment. This model can be interpreted as the description of a population of one species in an association, consisting of weakly connected populations (other interpretations are also possible). Usually such a model is described by the logistic equation.

In what sense can we talk here about stability? Evidently only in the sense of the probability that the population will degenerate during random variations in the environment, and in terms of the natural growth and competitive ability coefficients. But in such formulation the problem remains complex. Therefore, we will simplify it, and justify the following probable statement. If we consider the population as a system of independent particles that subdivide, for each of which the probability of death is given, the probability that the population will degenerate as a whole decreases exponentially as the number of individuals increases. On the other hand in the steady state phase, when the number of individuals is greatest, the competition among them is so keen and the behavior of the population as a whole is so determined, that very strong disturbances which affect the dynamic structure of the population are needed in order that the population degenerate. All this indicates that the logarithmic growth phase sector is most dangerous from the standpoint of degeneration when the number of individuals in the population is sufficiently small. Therefore, we will consider the model of a homogeneous population in the form

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$$\frac{dN}{dt} = a(t)N. \quad (209)$$

What effect do random fluctuations in the population size have on population growth? Suppose that these fluctuations are described by the distribution $\varphi(t)$ with mean zero and variance σ^2 . Then instead of (209) we will have

$$\frac{dN}{dt} = a(t)N + \eta(t)\sqrt{N} \quad (210)$$

(the mean fluctuation is proportional to the square root of the population size).

Introducing the new variable $\xi = 2\sqrt{N}$, we obtain from (210)

$$\frac{d\xi}{dt} = \frac{1}{2} \alpha \xi + \varphi. \quad (211)$$

Integrating, we have

$$\xi = \xi_0 e^{\frac{1}{2} \int_0^t \alpha(\tau) d\tau} + \int_0^t \varphi(\tau) e^{\frac{1}{2}(\Psi(t) - \Psi(\tau))} d\tau, \quad (212)$$

where $\Psi(t) = \frac{1}{2} \int_0^t \alpha(\tau) d\tau$.

If α is independent of time,

$$\xi = \xi_0 e^{\frac{1}{2} \alpha t} + \int_0^t \varphi(\tau) e^{\frac{1}{2} (t-\tau)\alpha} d\tau. \quad (213)$$

The mean value of ξ is equal to

$$\bar{\xi} = \bar{\xi}_0 e^{\frac{1}{2} \alpha t}, \quad (214)$$

since, by hypothesis, $\bar{\varphi}(t) \equiv 0$ and $\bar{\xi}_0$ is the expected value of the quantity $\sqrt{N_0}$ for the initial conditions which can be specified in terms of some distribution. For simplicity we will assume that the dispersion ξ_0 is zero, i.e., $\xi_0 = \bar{\xi}_0$. For the variance $\sigma^2(\xi)$ we obtain

$$\sigma^2(\xi) = \frac{\sigma^2}{\alpha} (e^{\alpha t} - 1). \quad (215)$$

To obtain the expressions for the mean ξ and the variance we can use the central limit theorem, assuming that the values of φ are mutually independent at different instants of time.

If $\varphi(t)$ is normally distributed, ξ has also a normal distribution with mean $\bar{\xi}_0 e^{\frac{1}{2} \alpha t}$ and variance $\frac{\sigma^2}{\alpha} (e^{\alpha t} - 1)$. The population size $N = \frac{1}{4} \xi^2$ has a χ^2 distribution with one degree of freedom with mean

$$\bar{N} = N_0 e^{\alpha t} + \frac{\sigma^2}{4\alpha} (e^{\alpha t} - 1). \quad (216)$$

This distribution is skewed (to the left) and therefore $N < \bar{N}$ with a high probability. This means that when the population size fluctuates randomly, its true values will almost always be less than its mean values. At the same time if $\alpha > 0$ (i.e., the population grows) the random fluctuations increase the mean population size. This follows directly from (216).

Finally in a growing population ($\alpha > 0$), random fluctuations in the population size increase on the average the stability of the system (by increasing the mean population size), but they also increase the probability that it will degenerate by decreasing the statistical stability (reliability) of the system, since $N < \bar{N}$. Here there is no contradiction, because we are talking about two different types of stability. In the first case we are dealing with dynamic stability, and in the second case with the probability of finding the system in a certain state. The inequality $N < \bar{N}$ indicates that for small values of the mean population size, the random fluctuations almost always lead to degeneracy.

What effect do random fluctuations in the natural growth coefficient have on the dynamics of the population size? It follows from (209) that

$$N(t) = N_0 e^{\int_0^t \alpha(\tau) d\tau} \quad (217)$$

If $\alpha(\tau)$ is normally distributed with mean $\bar{\alpha}$ and variance $\sigma^2(\alpha)$ which are independent of time, $\int_0^t \alpha(\tau) d\tau$ is also normally distributed with mean $\bar{\alpha}t$ and variance $\sigma^2(\alpha)t$ (by the central limit theorem, on the assumption that the values α are mutually independent at different instants of time). Then the quantity N/N_0 has a log-normal distribution with the same mean and variance, so that

$$f\left(\frac{N}{N_0}\right) = \frac{N_0}{\sigma^2(\alpha) N \sqrt{2\pi t}} \exp \left\{ -\frac{\left[\ln \frac{N}{N_0} - \bar{\alpha}t \right]^2}{2\sigma^2(\alpha)t} \right\} \quad (218)$$

This function has a unique maximum when $N^* = N_0 e^{(\bar{\alpha} - \sigma^2(\alpha))t}$. This implies immediately that if $\bar{\alpha} < \sigma^2(\alpha)$, then as $t \rightarrow \infty$ $N^* \rightarrow 0$ and the mode of the distribution for N shifts to the left, if $\bar{\alpha} > \sigma^2(\alpha)$, it shifts to the right. This means that when $\bar{\alpha} < \sigma^2(\alpha)$ the probability that the system will degenerate over time increases, tending in the limit to one; in the statistical sense

the system is not stable. When $\bar{\alpha} > \sigma^2(\alpha)$ and as $t \rightarrow \infty$, the probability that it will degenerate tends to zero, and in this case the system is stable.

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It is interesting to note that the fact that a population size subject to random fluctuations in the growth coefficient has a lognormal distribution implies that to preserve the population and its growth it is not sufficient that the averaged coefficient $\alpha(t)$ be positive (i.e., that the integral $\frac{1}{t} \int_0^t \alpha(\tau) d\tau$ be greater than zero for any t), a condition which is sufficient for ensuring growth in the deterministic model (209). It is also necessary that the integral $\frac{1}{t} \int_0^t \ln \alpha(\tau) d\tau$ be positive. This means that the population dynamics when there are random fluctuations in the growth coefficient are determined not by its arithmetic mean (as in the deterministic model), but by its geometric mean. But since the geometric mean is always smaller than or equal to the arithmetic mean, the constraints on the growth coefficient which ensures the increase in the population size will be more stringent in a probabilistic model than in a deterministic model. Naturally, the stability region which is obtained according to some criterion on the basis of the deterministic model, will be wider than the analogous region in the probabilistic model. From this follows the practical recommendation: treat the stability results obtained from deterministic models with caution, since evidently the values are somewhat too high and the constraints formulated by these are weaker than those in probabilistic models.

4. Extremum Properties of Certain Mean Characteristics of Associations

We will consider a sufficiently general model of a biogeocoenosis

$$\frac{dN_i}{dt} = N_i \left(\epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right), \quad i = 1, 2, \dots, n. \quad (219)$$

If $\gamma_{ij} = \gamma_{ji} \geq 0$, we shall speak about a BGC (or an association) consisting only of competing (or coexisting) species. If $\gamma_{ij} = -\gamma_{ji}$, $\gamma_{ii} = 0$, we will speak about a generalized "predator-prey" system, in which all species are pairwise connected by trophic relations of the "predator-prey" type. When $n = 2$, we obtain the classical Volterra system, consisting of two species, one of which serves as food for the other. We will call the matrix $\|\gamma_{ij}\|$ the competition matrix of the association.

The model of an association consisting of n species, is often /139 written in the form (D'Ancona, 1954).

$$\frac{dN_i}{dt} = N_i \left(e_i - \frac{1}{\mu_i} \sum_{j=1}^n \alpha_{ij} N_j \right), \quad i = 1, 2, \dots, n, \quad (220)$$

with the claim that this form is more general than (219). However, this is not the case, which can be shown easily. We will transform in (219) the variables $N_i = \mu_i x_i$. Then (219) will be written in the form

$$\frac{dx_i}{dt} = x_i \left(e_i - \frac{1}{\mu_i} \sum_{j=1}^n \frac{\gamma_{ij}}{\mu_j} x_j \right), \quad i = 1, 2, \dots, n. \quad (221)$$

Clearly, except for differences in notation, (221) will coincide with (220). Thus, we cannot speak about greater generality of one form or another, since they are simply equivalent, and therefore all results obtained for (221) will also hold when the model is written in the form (220). The assumptions $\gamma_{ij} = \gamma_{ji}$ or, $\gamma_{ij} = -\gamma_{ji}$ are by no means more rigorous than $\alpha_{ij} = \alpha_{ji}$ or $\alpha_{ij} = -\alpha_{ji}$, the difference is that the measurement units for the biomass of each species are selected differently.

Suppose we are given a BGC consisting of n competing species of sizes N_i . Then $\gamma_{ij} = \gamma_{ji} \geq 0$. Of course, this is a great simplification, in real associations the competitive interrelations are far from symmetric. Nevertheless this assumption does not have a great effect on the behavior of the system as a whole --the qualitative picture is preserved. We will make the change of variables $\xi_i = 2\sqrt{N_i}$. Then (219) can be written in the form of the gradient rise equations for some function:

$$\frac{d\xi_i}{dt} = \frac{\partial W}{\partial \xi_i}, \quad i = 1, 2, \dots, n, \quad (222)$$

where

$$W = \sum_{i=1}^n e_i N_i - \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} N_i N_j = \frac{1}{4} \sum_{i=1}^n e_i \xi_i^2 - \frac{1}{32} \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} \xi_i^2 \xi_j^2, \quad (223)$$

which can be verified directly. Then, if the coefficients ϵ_i and γ_{ij} do not depend explicitly on time,

$$\frac{dW}{dt} = \sum_{i=1}^n \frac{\partial W}{\partial z_i} \frac{dz_i}{dt} = \sum_{i=1}^n \left(\frac{\partial W}{\partial z_i} \right)^2 \geq 0. \quad (224)$$

But this implies that the function W , which is computed along the trajectory is an increasing function, and if the BGC has a stable stationary state $\{N_i^*\}$, $i = 1, 2, \dots, n$ with finite values of the quantities N_i^* , W attains the maximum in this state. In addition to this also in the case when the system can have populations which are infinite, it evolves in such a way that the function W which is calculated for the given values of ϵ_i and γ_{ij} is an increasing (or at least nondecreasing) function. By analogy with population genetics, we will call W the mean adaptability function of the association. /140

Returning to the old variables, we obtain

$$\begin{aligned} W &= \sum_{i=1}^n \epsilon_i N_i - \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} N_i N_j, \\ \frac{dW}{dt} &= \sum_{i=1}^n N_i \left(\epsilon_i - \sum_{j=1}^n \gamma_{ij} N_j \right). \end{aligned} \quad (225)$$

The quantity $V = \sum_{i=1}^n \epsilon_i N_i$ characterizes in fact the rate at which

the biomass of the association increases in the case when there is no competition and when there are no limits on the resources. We can say that the quantity V defines the greatest reproductive rate of the association (since there are no restraints which check the growth of all population sizes making up the association). Taking into account everything that was said above, we will call V the reproductive potential of the association. Then the first formula in (225) can be rewritten in the form

$$W = V - \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} N_i N_j. \quad (226)$$

Thus, an increase in W in the evolution of the association can be interpreted as an attempt of the association to maximize its reproductive potential (the term V) and to minimize the mean effort on competition (the term $\sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} N_i N_j$ can be considered as an averaging of the competitive ability coefficient γ_{ij} over all species in the association).

It is easily seen from the second formula in (225), that the quantity dW/dt decreases as the association evolves, and vanishes in the steady state. In its structure this quantity resembles strongly the variance, and in fact it characterizes the species diversity in the association in the degree necessary to ensure the evolution of the association as a whole.

We will now consider a generalized system of the "predator-prey" type, i.e., a model of an association in which $\gamma_{ij} = -\gamma_{ji}$. This means that the trophic relations between pairs of "predator-prey" species are symmetric. We will make the following change of variables: $\eta_i = \ln \frac{N_i}{N_i^*}$, where N_i^* is the positive solution of the system of equations

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$$\sum_{j=1}^n \gamma_{ij} N_j = \varepsilon_i, \quad i = 1, 2, \dots, n.$$

Then (219) can be written in the form

$$\frac{d\eta_i}{dt} = \sum_{j=1}^n \gamma_{ij} \frac{\partial G}{\partial \eta_j}, \quad i = 1, 2, \dots, n, \quad (227)$$

where

$$G = \sum_{i=1}^n N_i^* (\eta_i - e^{\eta_i}),$$

which can be verified directly. We calculate the total derivative G with respect to time

$$\frac{\partial G}{\partial t} = \sum_{i=1}^n \frac{\partial G}{\partial \eta_i} \frac{d\eta_i}{dt} = \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} \frac{\partial G}{\partial \eta_i} \frac{\partial G}{\partial \eta_j}. \quad (228)$$

But since $\gamma_{ij} = -\gamma_{ji}$, the quadratic form (228) is identically equal to zero. Consequently, the function G is an integral of system (227). The quantity G does not vary along any trajectory of the system. In the variables N_i , we obtain

$$G = \sum_{j=1}^n N_j \ln N_j - \sum_{j=1}^n N_j - \sum_{j=1}^n N_j^* \ln N_j^*. \quad (229)$$

Since G is determined with an accuracy up to a constant, (229) can be written in the form

$$G = S - M, \quad (230)$$

where $S = \sum_{j=1}^n N_j^* \ln N_j$ is a term which resembles in structure information entropy, which we will call the "quasientropy" of the association, and where $M = \sum_{j=1}^n N_j$ is the total biomass of the association. Thus, for sufficiently large N_j , the function G cannot remain constant when all N_j vary monotonically, and periodic solutions must exist, a fact we already know from the qualitative analysis of the "predator-prey" system. Since $G = \text{const}$, an association of this type evolves in such a way, that when the total biomass increases the diversity of the association which is characterized by its "quasientropy" must also increase.

Finally, we will consider a BGC model of a general type, when there are no constraints on the γ_{ij} . Suppose that the BGC has a nontrivial equilibrium position, so that all $N_i^* > 0$. Under which conditions will this position be stable? We write down the equations for the first approximation ($x_i = N_i - N_i^*$). From (219) we obtain

$$\frac{dx_i}{dt} = -N_i^* \sum_{j=1}^n \gamma_{ij} x_j, \quad i = 1, 2, \dots, n. \quad (231)$$

A necessary and sufficient condition that the equilibrium position be stable is that the real parts of the eigenvalues of the matrix $\| -N_i^* \gamma_{ij} \|$ be negative. But the eigenvalues ν_i of this matrix

are expressed in terms of the eigenvalues λ_i of the competition matrix as follows:

$$v_i = -N_i^* \lambda_i, \quad i = 1, 2, \dots, n.$$

Hence, a necessary and sufficient condition for the stability of the equilibrium position is that all eigenvalues of the matrix $\| \gamma_{ij} \|$ be positive. But then the quadratic form

$$\frac{dG}{dt} = \sum_{i=1}^n \sum_{j=1}^n \gamma_{ij} \frac{dG}{d\eta_i} \frac{dG}{d\eta_j} \quad (232)$$

must be positive-definite and $dG/dt \geq 0$, and the equality will only hold when $dG/d\eta_i = 0$, $i = 1, 2, \dots, n$, i.e., in equilibrium, or when $\gamma_{ij} = -\gamma_{ji}$, but then $dG/dt = 0$ everywhere on the trajectory.

Since near the steady state $G > 0$, and $dG/dt \geq 0$, by analogy with mechanics, the function $H = -G$ can be called the "energy" of the association. Then when the association evolves to nontrivial equilibrium, its "energy" decreases monotonically, and tends to its smallest possible value, or it does not change at all, but then the system may have closed trajectories.

Since $\frac{dG}{dt} = \frac{dS}{dt} - \frac{dM}{dt} \geq 0$ it follows that during the evolution of the association the rate at which its diversity increases must be at least as fast as the rate at which the total biomass M increases, since $\frac{dS}{dt} \geq \frac{dM}{dt}$. If the total biomass of the association decreases, the diversity of the association may also decrease.

We note that this result is evidently also valid in the case when some $N_k^* = 0$. But this is only an assumption which we have not yet proved. In this case the corresponding eigenvalues $v_k = 0$, and to study stability we must study the equation for higher order approximations.

Since $\frac{dG}{dt} \geq 0$, in the stable equilibrium state $G^* = \max_{N_i} G$.

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This implies immediately that the function

$$L = G - G^* = \sum_{j=1}^n N_j^* \ln \frac{N_j}{N_j^*} - \sum_{i=1}^n (N_i - N_i^*)$$

can be considered as a Lyapunov function for the system of equations which are the model of the BGC. In fact, $L \leq 0$, $dL/dt \geq 0$, and L is continuous together with its partial derivatives with respect to N_i .

Finally the state of the association can be characterized by its "energy" where the association is more stable the lower the amount of energy. Unfortunately, to calculate it we must know the equilibrium position of the system. It is interesting that the expression for the "energy" contains terms, which in structure are very similar to the "diversity" formula for the association.

5. The Number of Species in the Association

A very interesting problem is the problem of determining from the parameters of the model the number of species which may co-exist in the association. In presenting this problem we will mainly follow the work of Levins (Levins, 1968). We rewrite model (219) in the form

$$\frac{dN_i}{dt} = \frac{e_i N_i}{K_i} \left(K_i - N_i - \sum_{j \neq i}^n \alpha_{ij} N_j \right), \quad i = 1, 2, \dots, n, \quad (233)$$

where $K_i = \frac{e_i}{\gamma_{ii}}$ (we assume that $\gamma_{ii} > 0$). The quantity K_i can be called the "capacity" of the environment for the i -th species. The "capacity" is nothing else but the greatest population size of the i -th species. In fact, if there is no competition among the species ($\gamma_{ij} = 0$ for $i \neq j$), then $\max N_i = K_i$. It is assumed that the association consists only of competing species, i.e., that all $\gamma_{ij} > 0$ (and correspondingly, $\alpha_{ij} > 0$). By definition $\alpha_{ii} = 1$. The equilibrium values of the species population sizes in the association are determined from the solution of the system

$$K_i = N_i + \sum_{j \neq i}^n \alpha_{ij} N_j, \quad i = 1, 2, \dots, n. \quad (234)$$

This state can be characterized by a discrete distribution $f(N_j)$ for the population sizes. Applying the averaging operation using this distribution to both members of (234), we obtain

$$\frac{\bar{K}}{\bar{N}} = 1 + (n-1) \left[\bar{\alpha} + \frac{\text{cov}(\alpha_{ij}, N_i N_j)}{\bar{N}} \right]. \quad (235)$$

Here \bar{K} is the mean capacity for the association, \bar{N} is the mean number of individuals in the association, $\bar{\alpha}$ is the mean value of a quantity which characterizes the interspecific competition, $\text{cov}(\alpha_{ij}, N_i N_j)$ is the covariance between the interspecific competition characteristics and the size of the species. /144

Equation (235) is the basic equation which relates certain average characteristics of the association to the number of species in it. Unfortunately, we were not able to obtain a simple expression for the covariance. Therefore, we will make one simplifying assumption, namely, that $\text{cov}(\alpha_{ij}, N_i N_j) \ll \bar{\alpha} \bar{N}$. This means that either the coefficients α_{ij} or the quantity N_j differ little from their mean values for the entire association as a whole, or that the values of N_j do not depend much on interspecific competition (a system of weakly interacting species). Then, from (235) we obtain

$$n = 1 + \frac{\bar{K} - \bar{N}}{\bar{\alpha} \bar{N}}. \quad (236)$$

It is seen from this equation that when $\bar{\alpha}$ increases, the number of species in the association is reduced in the same way as when the mean size of the association is increased. When the mean capacity of the association increases, the possible number of species also increases. At least one species will always exist in the association.

If the covariance is different from zero, the number of species will depend on the character of the competitive interrelations. For a negative correlation (the covariance is negative) the number of species increases, for a positive correlation it decreases.

When new species are formed in the association, what effect do these have on the stability of the association as a whole? When a new association is formed as a result of random immigration, the α_{ij} can be considered to be independent random variables, except that they may be correlated with the α_{ji} . During competition both these quantities will be positive; in relations of the "predator-prey" type they will have opposite signs. To simplify the situation, we assume that the mean values

of the α_{ij} are equal to zero. Then

$$\bar{D}_n = \bar{D}_{n-1} - (n-1) \text{cov}(\alpha_{ij}, \alpha_{ji}) \bar{D}_{n-2}. \quad (237)$$

Here \bar{D}_n is the mean value of the determinant of the matrix $\|\alpha_{ij}\|$, $\bar{D}_{n-1} = D_{n-1}^i$, where D_{n-1}^i is the determinant obtained from D_n by eliminating the i -th row and the i -th column and the averaging takes place over all i , i.e., over all species in the association.

It follows from (237), that the mean value of D_n becomes negative as n increases (if the covariance between α_{ij} and α_{ji} is positive). But if during stability (as we have shown above) the matrix $\|\gamma_{ij}\|$ and consequently also $\|\alpha_{ij}\|$ have positive eigenvalues, D_n must be positive. Then (237) gives an upper bound for the mean /145 number of species in the association as a function of the symmetry of the interactions. When the α_{ij} and α_{ji} are negatively correlated such upper bound does not exist.

For each species the mean population size is equal to

$$N_i \sim \frac{K_i}{\bar{D}_n} \{ \bar{D}_{n-1} - (n-1) \bar{\alpha} \bar{D}_{n-2} - \text{cov}(\alpha_{ij}, D_{n-2}^{ij}) \}. \quad (238)$$

In the beginning the covariance is zero. During evolution the removal must reduce the quantities α_{ij} , i.e., the sensitivity of the species to competition. However, the positive removal rate will be greatest for those α_{ij} for which D_{n-2}^{ij} has the largest value. Thus, removal will lead to negative correlations between α_{ij} and α_{ji} , and facilitate in this way an increase in the number of species in the association. Both the stability of the system and the probability of incorporating a new species will change.

The hierarchial structure of the association is determined by the covariance of the coefficients α_{ij} and α_{ji} and its non-homogeneity by their variances.

6. Artificial Closed Biosystems

It is known that entire systems of living organisms refer to so-called open or flow systems (Shepelev, 1966). The material-

energy base for the existence of living systems is the preservation of a stationary (equilibrium) state resulting from a continuous change and restoration of their chemical structure which is accompanied by losses and replenishments of internal energy reserves. Therefore such systems can only function under the condition that energy and substances arrive at the input to the system, and products of the vital activity are removed at the output.

Ensuring the vital activity of man as an open system (when life support systems are created for man in spaceship cabins) requires creation of reserves of substances he needs (oxygen, water, food) for the entire flight as well as the creation of devices for the storage of these reserves, the collection and removal of products of the organism's vital activity. All this is a serious obstacle in planning lengthy interplanetary flights.

In principle the possibility exists of creating man life-support systems which are potentially independent of weight and volume characteristics and the length of the flight. These are so-called closed-loop or closed systems. The principle for the existence of a closed biological system is based on the repeated use of a relatively small initial amount of chemical elements in a closed cycle in which the substances of the system itself are converted. Here in a closed system the vital activity products of man must be transformed through other living organisms into a form acceptable to man (into food, oxygen and water).

At the present time the principles and various variants used to construct life support systems on the basis of the biological cycle of substances are described in the literature (Shepelev, 1965; Gitel'zon, Terskov, 1965) where each stage in such a cycle utilizes various groups of microorganisms, algae, higher plants, and lower and higher animals. It is a characteristic feature of such life support methods that the vital activity of man is ensured not by creating means which exist independently of him, but by including man himself as a component in the system. /146

Figure 38 shows the basic scheme for the trophic relations in a closed biosystem (Shepelev, 1966).

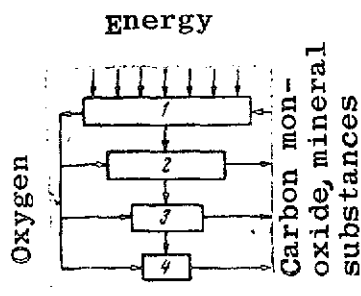


Fig. 38. Basic scheme of the trophic relations (1-4) in a closed biosystem.

In the energy sense the most important aspect of the cycle is the introduction of energy into the system from external sources, its transformation and accumulation in the form of organic compounds, which takes place on the first trophic level through plant photosynthesis. The second trophic level is occupied by plant-eating animals, which can serve as food for carnivorous animals ("predators" of first, second, etc., orders) which make up the third and successive trophic levels depending on the length of the food chain. We note that usually every trophic level is simultaneously occupied by several competing species.

Finally, the last stage in the food chain are various heterotrophic microorganisms which complete the process of destroying the organic substances and convert them into inorganic compounds used again by the plants in the next cycle in which the organic substances are synthesized and the energy is accumulated.

Since the substance and the energy transfer from one trophic level to another takes place with considerable loss of energy, the successively reduced areas of the rectangles in Fig. 38 denoting the different trophic levels illustrate this process.

It should be noted that the scheme for the closed cycle of matter in such an artificial biological system is basically similar to the matter cycle in the biosphere (a closed man life-support system in a spacecraft cabin is a model for the earth's biosphere). Therefore, it is worthwhile to consider common properties of the natural original which must be modeled under spacecraft conditions--the earth's biosphere and its elementary units the biogeocoenoses--from the standpoint of the possibility or usefulness of reproducing these in the model. The modeling and the calculation of closed biosystems can be carried out using the "portrait" modeling approach in which the models used are real almost completely isolated biosystems which exist in nature--biogeocoenoses and various unions of these. But a complete copying of the biogeocoenosis cannot be successful, since the criteria for natural associations and for artificially created associations may be different. Evidently only if the main organization principles of natural biosystems and their functional mechanisms are copied and considered in the most general form, can we expect success.

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CONCLUSION

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In conclusion we would like to summarize briefly what was done and point out what still needs to be done, without making a particular effort but using the rules which were presented above. In addition to this we would like to formulate a number of sufficiently general problems, the solution of which promises to give

interesting results. We note that in this book we used only known methods, but we applied them to models which are not well known, and in the process we confined ourselves to the simplest cases without using, for all practical purposes, the capabilities of contemporary electronic computer technology.

Like any sufficiently complex system (for example, economics provides examples of such systems), the BGC belongs to a class of systems which we now call "large systems." We note, however, that almost all methods which are used when these systems are investigated are not related to specific features of these systems reflecting the tremendous number of variables and parameters which describe them. They can also be applied to problems of small dimensionality, and the larger dimensionality leads only to greater complexity of the solution (what Bellmann called fittingly the "curse of dimensionality"). Therefore, we restricted ourselves to problems of small dimensionality, where at the expense of generality we gained in clarity.

On the other hand, even though the BGC is a system which consists of hundreds and thousands of populations of various species, each of which in turn is also a sufficiently complex system, it can be characterized with a certain degree of accuracy even though only roughly by one phase variable and two or three parameters and its evolution over time can be described by one differential equation. This was described in sufficient detail in Chapter I. Of course, here we are immediately confronted with the question of selecting properly this variable (or variables) and of the degree of the correspondence between the model which was set up and the real BGC and the correct definition and "measurement" of the parameters which enter the model. Here two approaches are possible. The first is to describe the association as fully as possible: its species composition, the population density, the biomass or the population size, etc. But to determine the BGC structure, it is not enough if it is described only at one instant of time, a sufficiently complete dynamic description must be given, and the amount of information which must be stored increases sharply. The model which is constructed from this data serves only as a more compact record. Of course, it can also be used for other purposes (for example, to solve optimization problems). Nevertheless, because of its excessive concreteness this model has too narrow a range of application.

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In the second approach when the model is constructed only the most general laws are used, the model is "applied" to a concrete BGC by selecting the appropriate parameter values which enter the model. Then, when we study a concrete BGC we already know that we must "measure" and the selection of particular characteristics for the study is entirely determined by the model.

The checking of the degree of correspondence of the model, the determination of important variables and parameters is an independent, very complex and at the same time interesting problem, whose study is beyond the scope of our book.

We will give examples of certain problems which can be solved by the methods presented in the book.

1) The control of "harmful" animals is one of the problems of regulating the number of species which make up the BGC and of optimizing its structure. The criterion used here is usually the requirement that the number of individuals in the "harmful" species be minimized with constraints on the number of individuals in the other species. Various types of control are used. The most widely used means is the use of poisonous chemicals, which exterminate not only individuals in the "harmful" species, but also in the remaining species, of course, to a lesser extent if some selectiveness is present. The action can be of short duration (pulses) and continuous. If the BGC consists of n species and the first species is "harmful" then we can select for the criterion either

$$G_1 = \int_0^{\infty} N_1(t) dt,$$

or

$$G_2 = \alpha N_1(T) + \beta \frac{dN_1}{dt}(T),$$

where α and β are positive constants. We must find the control vector which minimizes G_1 or G_2 subject to constraints of the type

$N_2 \geq N_2^*, \dots, N_n \geq N_n^*$, where N_2^*, \dots, N_n^* are positive constants

which are given. Assuming that the mortality for individuals in each species is proportional to the concentration C of the poisonous chemicals, the control vector $q = \{q_1, \dots, q_n\}$ can be represented in the form

$$q_1 = \mu_1 C; \quad q_2 = \mu_2 C; \quad \dots, q_n = \mu_n C.$$

The control parameter in the given case is the concentration c . For a pulse action we can use a discrete model or a continuous model where the control is given in the form of a δ -function. Where we act continuously we can use the methods which were presented in the last chapter. Since we have only one control parameter to regulate the system consisting of n species, we can

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hardly expect great effectiveness and flexibility of this decision rule.

More promising and richer in possibilities are biological methods of "pest" control. The biological control of the size of the "harmful" species can be realized in two ways: either by changing the trophic structure of the given BGC by introducing into it a "predator" for which the "pest" is a "prey" or one of its parasites, or by acting directly on the reproduction of this species, for example, by introducing into its population individuals with genetically impaired fertility. Problems of the first type can be formulated and solved immediately, using the methods presented in this book. In this case we are dealing with the classical "predator-prey" situation. The difference is that above we only considered the yield collection process, the removal of individuals from the system, and the decision was always positive, while here "predators" are added to the system so that the decision becomes negative.

When it is regulated genetically individuals from the same species are introduced into the population, but with a modified chromosome apparatus, which introduces considerable disturbance to the reproduction process of the "pests." This method was developed for the first time by A. S. Serebrovsky (1940), who proposed that translocations which can exist in the homozygous state be used. Later it was also proposed to use in practice individuals which were heterozygous in the recessive lethal gene or sterile (in the so-called "Curacao method" sterile males were introduced). To solve problems of this type models are needed which take into account the genetic diversity of the individuals in the population of one species and different types of relations between the sexes.

The formulations of the problems can be simplified considerably if we assume that the process is stationary. In this case we seek such constant or periodically repeated action which will ensure the fastest reduction in the "pest" species while the entire BGC "does not deteriorate," i.e., we seek $\min \left\{ \frac{dN_1}{dt} \right\}$

(for a discrete model $\min [N_1(h) - N_1(0)]$ with the constraints: $dN_2/dt \geq 0$, $dN_3/dt \geq 0$, . . . , $dN_n/dt \geq 0$ (for the discrete model: $N_2(h) \geq N_2(0)$, $N_3(h) \geq N_3(0)$, . . . , $N_n(h) \geq N_n(0)$). Having solved such a problem we will find the rate of flow for the corresponding individuals in the BGC, for which the "pest" species dies out in the shortest possible time.

It is clear that the possibilities of such decisions, which change the structure itself, the character and the size of the reproductive and competitive relations are much wider than those of

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decisions based on the direct annihilation of "harmful" individuals.

2) Another example of problems in which the decision is negative and the process is the opposite of collecting the yield is the establishment of a more advantageous equilibrium state by increasing artificially the number of some species. For example, in a "predator-prey" system the amount of yield collected can be substantially increased by the timely introduction of new individuals.

3) Optimal feed diet problems became classical problems a long time ago in linear programming (Dantzig, 1966). However, in these it is assumed that the whole feed is eaten, without any preference, and the criterion function is usually the cost of the feed. In natural biological systems, the "predator" is most often a polyphage which feeds on several "prey" species with various degrees of preference. It is clear that when the optimal feed diet is prepared for such an object (for example, a fish pond) this fact must be taken into account and the appropriate corrections must be introduced into the Volterra model, where it is assumed that the rate at which the "predator" consumes the "prey" is proportional to the number of encounters of the "predator" with the "prey."

The experimental data of V. S. Ivlev (Ivlev, 1955) which were worked out by V. S. Ten, have shown that in the case when the "predator" can feed on several species of "prey" the Volterra assumption about the feeding mechanism of the "predator" is only valid when the total number of "prey" is very small. Starting from a certain level, the "predator" displays a selective capacity during the encounter with a particular "prey" species, so that certain species become dominant in his diet. The percentage of "prey" which was eaten from the total number encountered will be called the "predator's strategy, and we will denote it by $k\{k_1, k_2, \dots, k_n\}$. The rate at which the "predator" consumes every "prey" species $\vec{v} \{v_1, v_2, \dots, v_n\}$ depends essentially both on the selected strategy k and on the sizes N_1, \dots, N_n .

The polyphagy principle proposed by V. S. Ten states that the "predator" selects a strategy k for which the functional

$$I = \sum_{i=1}^n c_i v_i(k, N_i); \quad i, j = \overline{1, n}$$

attains a maximum. The strategy may be called optimal. Here the c_i are constants which characterize the "value" of the i -th "prey" species in the "predator's" diet.

Suppose that the following assumptions are valid: 1) the BGC is in a stationary state ($N_i = \text{const}$, $i = \overline{1, n}$), 2) the "predator" when he goes hunting encounters a "prey" from the i -th species with a certain frequency λ_i , and eats only a part (k_i) of the number of individuals encountered in the time τ_i , 3) the frequencies λ_i are proportional to the sizes N_i . If we introduce the concept of the relative "cost" of the "prey" from the i -th species

$$\bar{c}_i = \frac{c_i}{\tau_i},$$

the quantities \bar{c}_i can be considered as preferential food characteristics. If $\bar{c}_i = \bar{c}_j$, the trophic relation of the "predator" to "prey" from species i and j is the same, i.e., $k_i(\lambda) = k_j(\lambda)$. The "predator" gives preference to "prey" with the largest value \bar{c}_i .

Thus, if the relative costs are arranged in a decreasing sequence

$$\bar{c}_1 > \bar{c}_2 > \dots > \bar{c}_n,$$

the optimal strategy of the "predator" will be as follows:

1. If $N_1 = N_2 = \dots = N_n = \text{const}$, then if the total concentration of the "prey" is sufficiently high, the "predator" eats only the first species with the largest cost \bar{c}_1 .
2. If $N_1 \leq N_2 \leq \dots \leq N_n$, then in the case when $N_{i-1} \leq N_i < N_{i+1}$, individuals from the first i species are eaten, species $i + 1, \dots, n$ are rejected.
3. If the relative concentrations of the "prey" are constant, and their total absolute number increases, when the number is small all species are consumed, and when the absolute number increases all species are rejected successively except the first, first the n -th species with the minimum relative costs \bar{c}_n , then the $(n - 1)$ -th species, etc.
4. Since the BGC is a system consisting of hundreds and thousands of elements which are related sufficiently closely, evidently certain quantities exist which can fully characterize the average behavior of the entire system. In statistical

mechanics, for example, such quantities are the temperature, the internal energy, etc. We talk about creating a certain statistical mechanics analogue of a system such as a BGC. In the first approximation we can assume that the components of the BGC are described by the system of equations of the Volterra model, where the order of the system itself is sufficiently high. The difficulty is that in contrast to the equations of mechanics, the general system of Volterra equations is not Hamiltonian.

5. In addition to the equations which describe the dynamics of the biomass, the BGC model must include equations which describe flows of inert matter and energy. The presence of photosynthesis gives rise to intense gas exchange, and, in addition, also other processes in the BGC are accompanied by various gas flows. Industry and the building of residential quarters in the region of the given BGC shift the equilibrium of the gas flows which were formerly in a steady-state. Thus, the problem arises naturally of supplementing optimally the BGC by plants with given constraints on the composition of the atmosphere in this region. The flows of various chemical substances in the soil, the determination of the characteristics of the stationary concentration distributions for the given soil profile are also very important in characterizing the BGC. The introduction into this system of various chemical compounds (fertilizer, radioactivity, etc.) can shift in various ways the existing distribution. Here we have also a number of interesting optimization problems.

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